

SYSTEMATIC STATUS, VARIATION AND DISTRIBUTION OF FOUR
MIDDLE AMERICAN CICHLID FISHES BELONGING
TO THE *AMPHILOPHUS* SPECIES GROUP,
GENUS *CICHLASOMA*¹

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ABSTRACT: *Cichlasoma longimanus*, *C. margaritiferrum*, *C. rosstratum* and *C. robertsoni* form a complex within the *Amphilophus* species group. Their taxonomic history is reviewed and synonymies presented. *Cichlasoma popenoei* Carr and Giovannoli is placed in the synonymy of *C. longimanus*. *C. margaritiferrum*, known only from the type, is maintained as a valid species.

Geographic variation of meristic, morphometric and color traits is discussed, but subspecies are not defined. Coloration in life, sexual dimorphism, juvenile distinctions and ecology are discussed for each species. A key is provided to distinguish the four species.

The roles of historic events and competition are discussed in relation to present geographic distribution.

INTRODUCTION

The first cichlids to reach Central America from South America in the Late Mesozoic or Early Cenozoic have since given rise to several phyletic lines which were recognized as "sections" of *Cichlasoma* by the only reviser, Regan (1905; 1906-08). Subsequent authors have treated these divisions as genera, subgenera or maintained them as non-taxonomic categories pending complete revision of *Cichlasoma*.

During our studies of Middle American cichlids, we have found Regan's divisions of *Cichlasoma* very useful and, in large part, representative of phyletic groupings. Nevertheless, Regan's keys to *Cichlasoma*, still the only comprehensive ones available, often fail in practice, now that considerably more material of wide-ranging species is available. Hubbs' (1936) detailed account of *Cichlasoma urophthalmus* from Yucatán is still the only attempt to examine the geographic variation of a Middle American cichlid. It is now possible to determine the complete range of many Middle American fishes, and to make decisions regarding their relationships. The present study is an attempt to clarify the status of four species, which comprise the *longimanus* complex of the *Amphilophus* group, until *Cichlasoma* and allied genera can be thoroughly revised. Studies of the *Cichlasoma nigrofasciatum* and *C. dovii* complexes are in preparation.

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Jordan, Evermann and Clark (1930) pointed out that the generic name *Amphilophus* Agassiz has priority over *Astatheros* Pellegrin if the species in the two groups are united. We follow Miller (1966) in referring members of the *longimanus* complex to the *Amphilophus* group. Most divisions or groups of *Cichlasoma* are represented by species heavily concentrated about the Río Usumacinta in southern Mexico and Guatemala (Miller 1966). Unlike others, the *Amphilophus* group is notable for its large southern, and Pacific slope representation. Sixteen species tentatively comprise the *Amphilophus* group: *Cichlasoma robertsoni*, *C. margaritiferrum*, *C. macracanthum* (Günther), *C. guija* Hildebrand, *C. heterodontum* (Vaillant and Pellegrin) and two undescribed species (Miller 1966) are confined to northern Middle America; *C. rostratum*, *C. altifrons* (Kner and Steindachner), *C. alfari* Meek, *C. lyonsi* Gosse, *C. calobrense* Meek and Hildebrand, *C. labiatum* (Günther) (probably including *C. lobochilus*, *C. erythraeum* and *C. dorsatum*), *C. citrinellum* (Günther) (probably including *C. basilaris* and *C. granadense*), and an undescribed species occur in southern Middle America; and *C. longimanus* has a wide central distribution. *C. atromaculatum* Regan and *C. ornatum* Regan from northern South America may also belong to this group.

Regan (1906-08) summarized many of the characters of Section *Astatheros* (preoccupied by *Amphilophus*) and others are included below: produced snout, upper profile of snout straight, maxillary not extending beyond vertical of anterior margin of eye; pectoral fins long, reaching origin of anal fin or far beyond; basic color pattern comprising five to nine cross bars on body.

We have chosen *C. longimanus*, *margaritiferrum*, *rostratum* and *robertsoni* for study because of their combination of common traits, which has led to confusion in the literature, and because they were in great need of comparative study. Other *Amphilophus* group species, such as *C. macracanthum* and *C. altifrons*, are similar, but can be distinguished fairly well using existing literature. *C. macracanthum*, which is sympatric with *longimanus*, is distinguished by its rounded caudal fin, free lower lip fold (no frenum, except in some juveniles), lower dorsal and anal spine counts, and little or no spotting on soft dorsal and anal fins. The *longimanus* complex, in addition to *Amphilophus* group traits has: a large lateral spot on the body over tip of pectoral fin, a smaller spot on caudal fin base, spotted soft dorsal and anal fins, truncate or slightly emarginate caudal fin, fold of lower lip interrupted (with frenum) and often bright blue spots or vermiculations on head and anterior body.

C. robertsoni and *longimanus* each have developed into several recognizable local races, which are sufficiently distinct to merit taxonomic recognition. We, nevertheless, have confined ourselves to clarifying distributions and relationships to species level. Although we have divided species into geographic units (Fig. 1) for analysis, these "Populations" do not necessarily correspond to subspecific units. A detailed analysis of geographic variation is not one of the objectives of this paper.

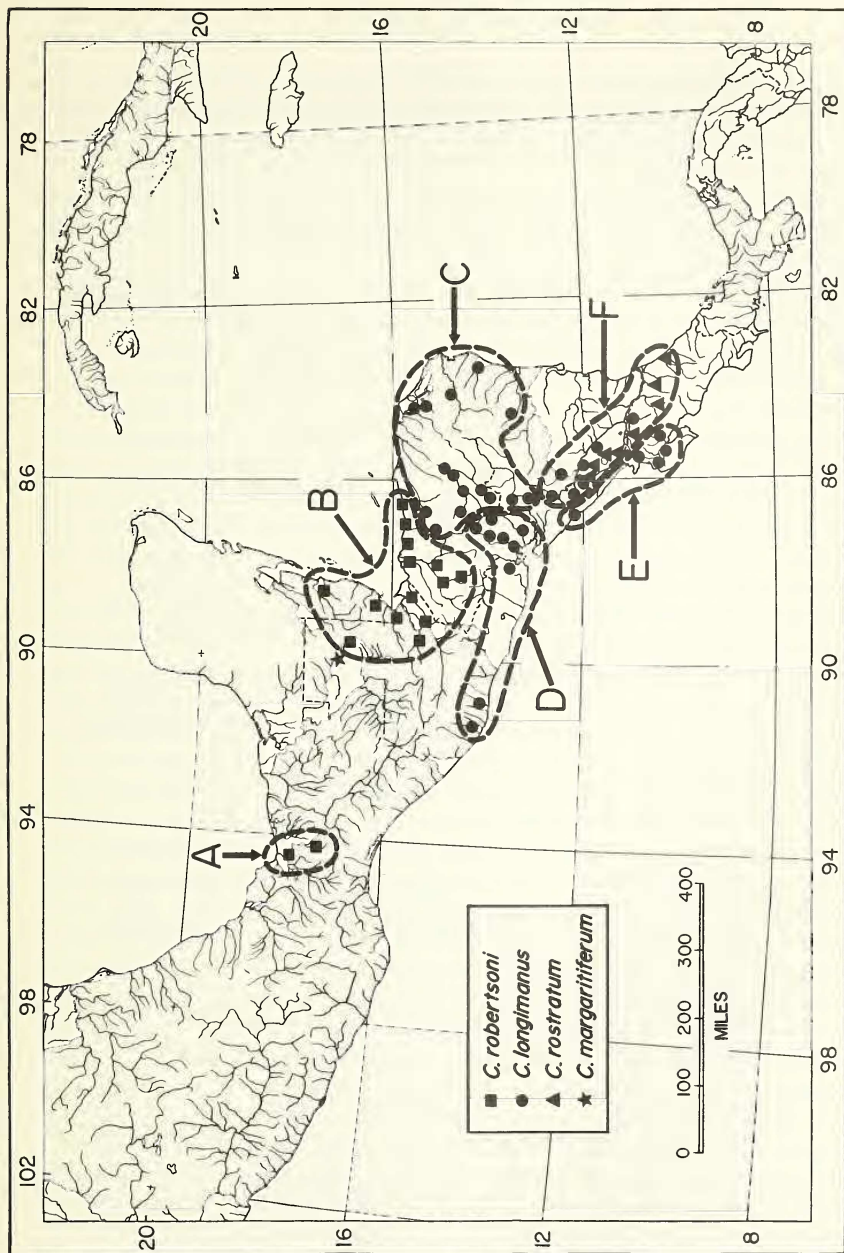


FIGURE 1. Major population samples of *Cichlasoma robertsoni*, *C. longimanus* and *C. rostratum* are lettered a through f. Each symbol represents a locality or localities of specimens analyzed in this study.

MATERIALS AND METHODS

We have examined 1,464 specimens of *C. longimanus*, 222 specimens of *C. rostratum* and 776 specimens of *C. robertsoni*, including the holotype of *C. popenoei*. Considerable data were obtained about the holotype and only known specimen of *C. margaritifera*, because of uncertainties regarding its status and distribution. We collected most material from all of Central America except Guatemala. Loan specimens largely from Mexico, Guatemala and British Honduras, supplemented our own collections.

Specimen localities were plotted on a map and grouped into six geographic units (Fig. 1) referred to as Populations A through F. On the basis of preliminary counts and measurements, an effort was made to adjust the boundaries of each Population to correspond to natural breaks in genetic continuity either at specific or subspecific level. Populations A and B lie entirely on the Atlantic versant and comprise northern and southern populations of *robertsoni*. Population C represents the Atlantic slope segment of *longimanus*, which recently has been in contact with Pacific slope *longimanus* through a Río Choluteca-Río Patuca connection. Populations D and E include a northern and southern Pacific segment of *longimanus*. Population F comprises an Atlantic allopatric population of *longimanus* and the Atlantic species, *rostratum*.

Initially 15 meristic counts and 21 body measurements were made and sex recorded on a minimum of 25 specimens from each Population (number of dorsal, anal, pectoral, pelvic and caudal soft and spinous elements; total gill rakers; pored scales in upper and lower lateral lines; longitudinal scales; scales above and below lateral line; caudal-peduncle scale count; and total vertebrae. Standard length, head length, orbit diameter, snout length, length of upper jaw, bony interorbital distance, suborbital width, body depth, least depth of caudal peduncle, length of caudal peduncle, predorsal distance, preanal distance, prepectoral distance, prepelvic distance, length of pectoral, pelvic and caudal fins, length of dorsal and anal fin bases, length of sixth and last dorsal spines). Specimens were selected from several localities within each geographic unit. These data were analysed and 12 meristic and 6 proportional measurements were found valuable in differentiating populations. Additional counts were made and meristic data were tabulated in geographic sequence for trend analysis within each Population. General intraspecific variation was discussed using these results. Counts from 100 specimens from throughout each Population (except 50 specimens from Population A) were used in preparing the graphs of meristic variation (Figs. 2 and 3). We use the term "significant" in discussing meristic variation between pairs of Populations in the sense of Hubbs and Hubbs (1953), regarding overlap of rectangles constructed from two standard errors on each side of the mean. Total vertebral counts (including hypural complex) for each species are based on fewer specimens (Table 1).

Proportions from approximately 50 specimens, throughout the size range of each species (*longimanus* from Atlantic and Pacific versants were analyzed separately) were used in preparing scatter graphs (Figs. 4-7). The fact that

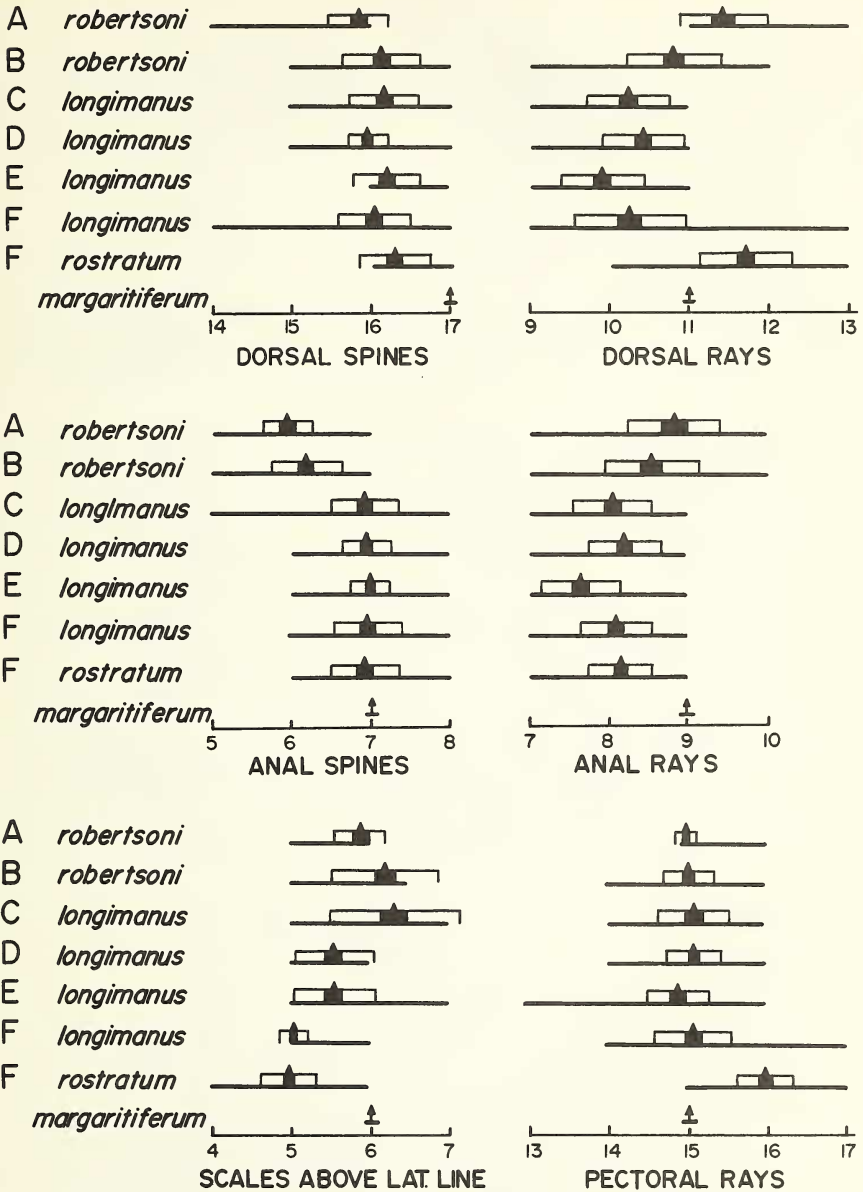


FIGURE 2. Meristic variation of populations of *Cichlasoma robertsoni*, *C. longimanus* and *C. rostratum*. The graphic presentation is that of Hubbs and Hubbs (1953), showing the range, mean, two standard errors on each side of the mean (black bar) and one standard deviation on each side of the mean (black and white bars). Meristics of the holotype of *C. margaritifera* are included.

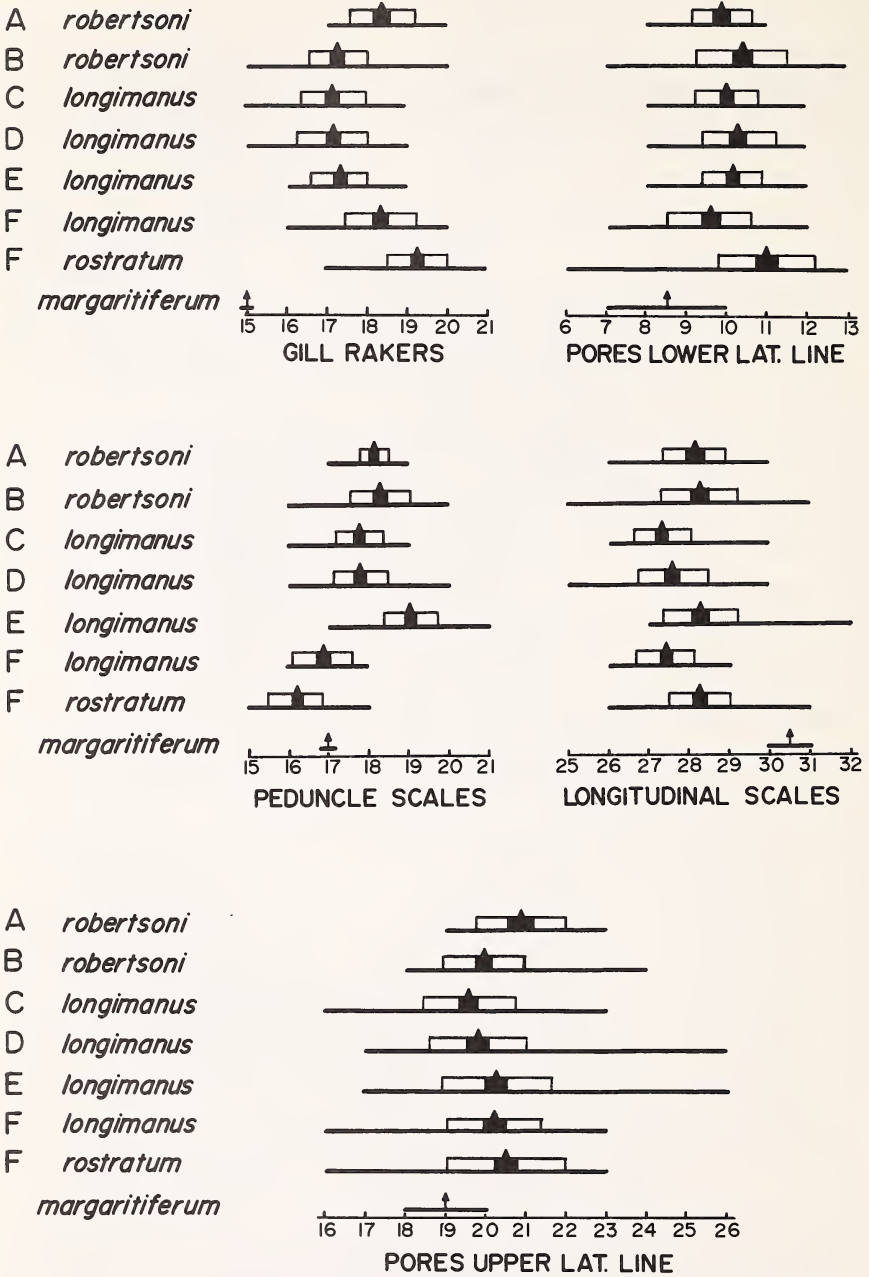


FIGURE 3. Meristic variation of populations of *Cichlasoma robertsoni*, *C. longimanus* and *C. rostratum*. See figure 2 for method of graphic presentation.

TABLE 1

Total vertebrae, including hypural complex, in *Cichlasoma rostratum*,
C. robertsoni and two major populations of *C. longimanus*

Species	Number of Vertebrae			
	27	28	29	30
<i>C. rostratum</i>		2	39	1
<i>C. robertsoni</i>			40	1
<i>C. longimanus</i> (C, D, E)	6	79	2	
<i>C. longimanus</i> (F)	5	24		

specimens were chosen from throughout each Population of each species, accounts in part for the wide spread of data of a few proportions. Three additional characteristics, angle and contour of dorsal profile and pectoral fin extension, are useful in distinguishing local populations of *longimanus*. Pectoral fin extension is the point on the body reached by the tip of pectoral fin and is measured by the anal fin element over which base it lies.

Counts and measurements conform to methods described by Hubbs and Lagler (1958) with one exception: the last two dorsal and anal rays are counted as one, only when closely approximated at the base; when the base of the last ray is not adjacent to the penultimate ray, each ray is counted separately. The following count and measurements are not defined in Hubbs and Lagler: longitudinal scales are counted commencing with first scale of row immediately below upper lateral line and terminating at end of hypural plate; preanal, prepectoral and prepelvic distances are measured from tip of snout to origin of each respective fin; length of caudal fin is the distance from end of hypural plate on midline to most posterior tip of caudal fin.

Life colors were recorded in the field from living material or obtained from color photographs of freshly captured specimens.

Sex was determined externally from the shape of the urogenital papilla, and confirmed on a random basis by gonadal inspection. Specimens less than 50 mm in standard length (SL) were found to be immature and not sexed.

The locality map (Fig. 1) shows all localities from where material was examined for the study. When several collections were made at a specific locality, only a single record appears on the map. The distribution map (Fig. 8) was based on specimens used in this study and previously unpublished records of specimens located at UMMZ and USNM.

The genus is often omitted from the scientific name of species treated in this study, when no confusion can incur. Although several nominal genera are discussed in the paper, only *Cichlasoma* is currently considered valid.

The majority of the collections have been deposited in the Natural History Museum of Los Angeles County (LACM) and the Museo de Zoología, Univer-

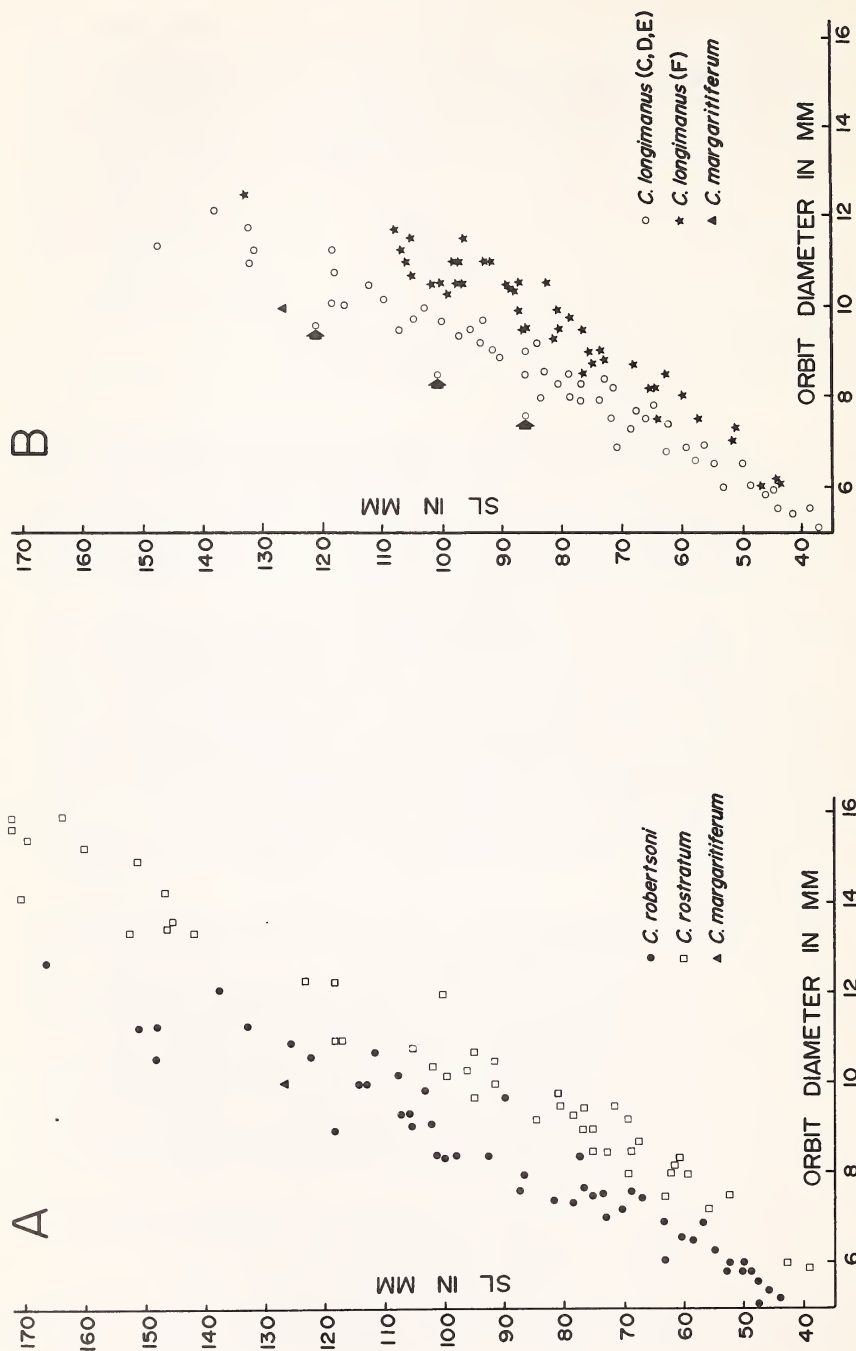


FIGURE 4. Orbit diameter in four species of *Cichlasoma*. Arrows in 4b indicate specimens from Finca Taboga, Costa Rica.

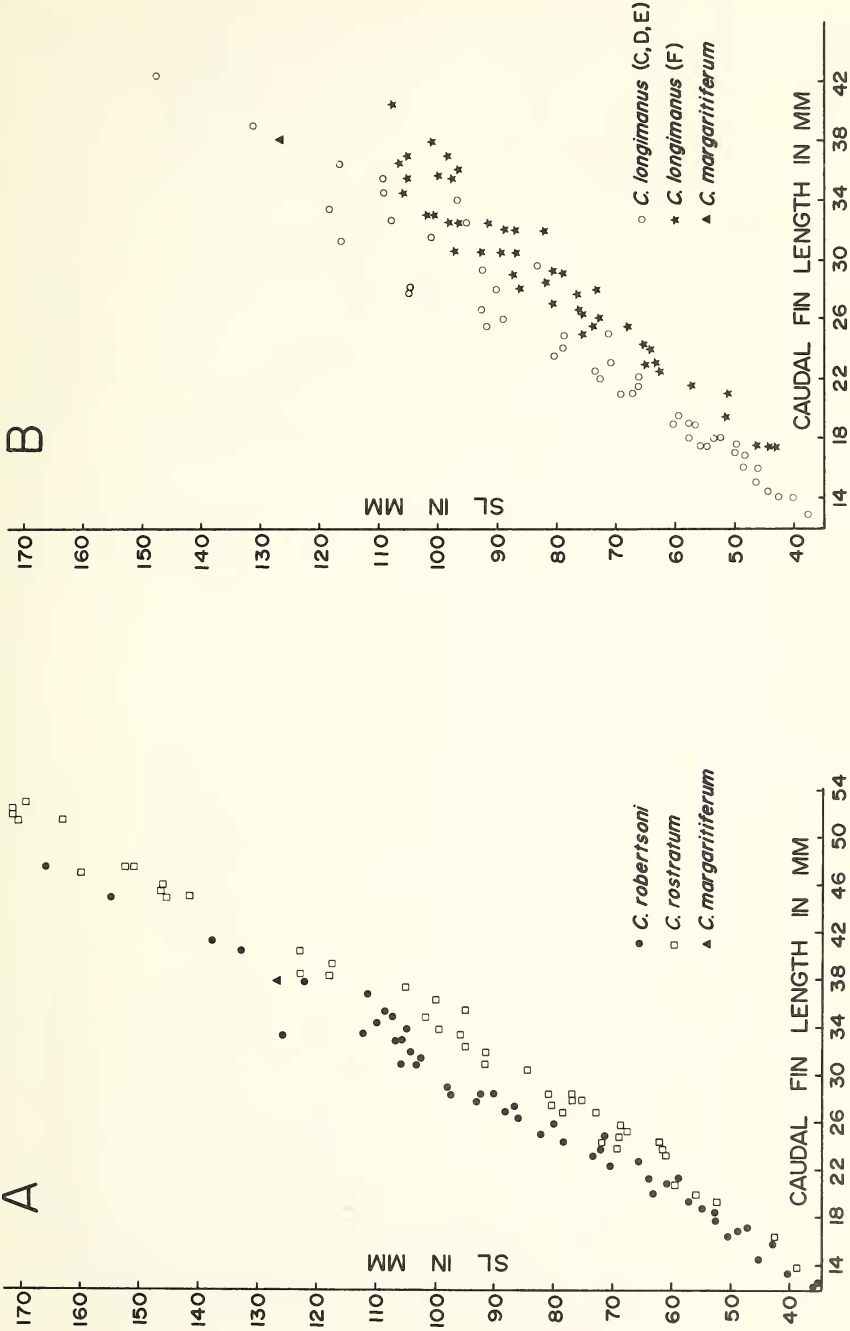
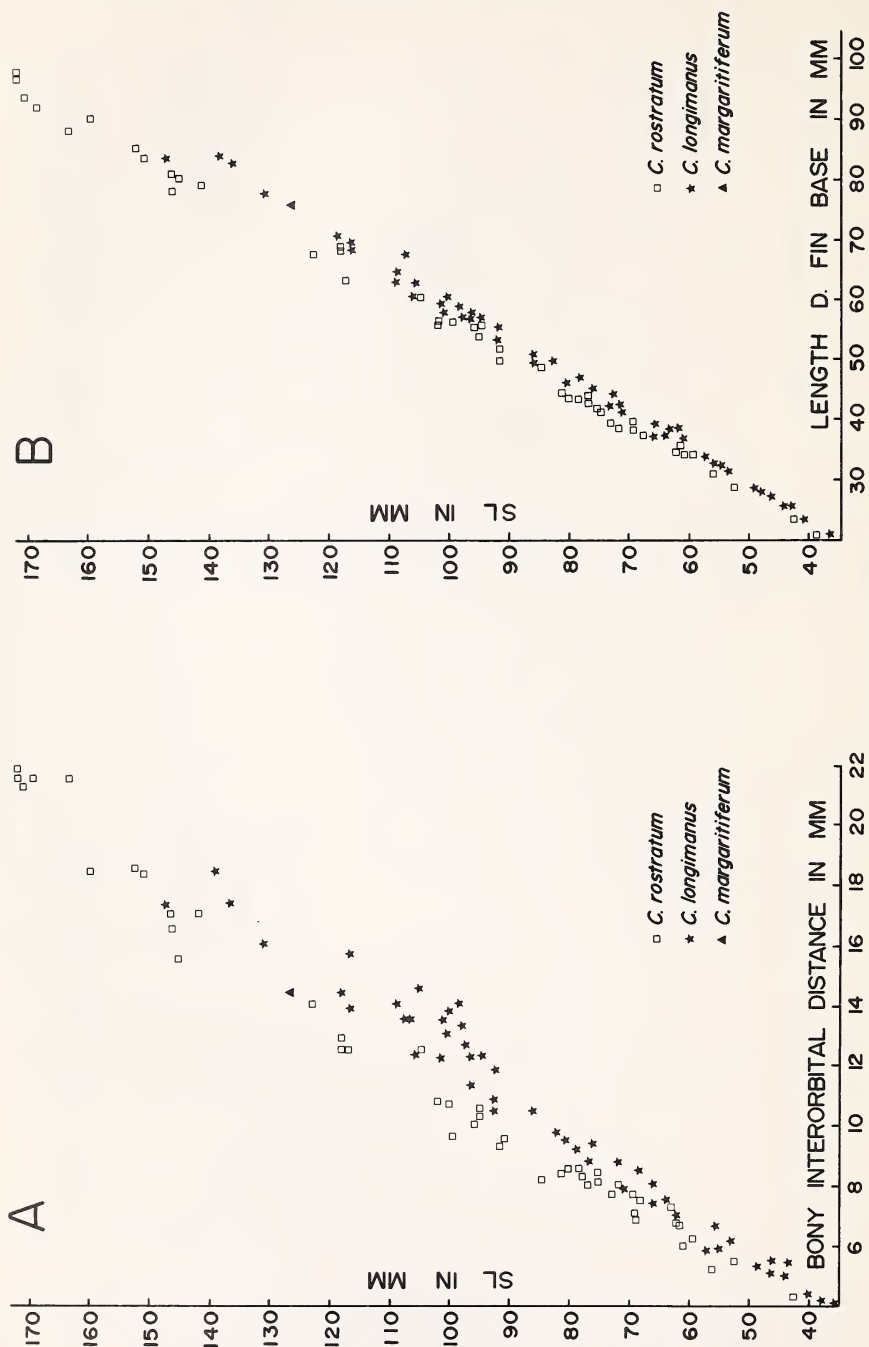


FIGURE 5. Caudal fin length in four species of *Cichlasoma*.

FIGURE 6. Interorbital distance and length of dorsal fin base in three species of *Cichlasoma*.

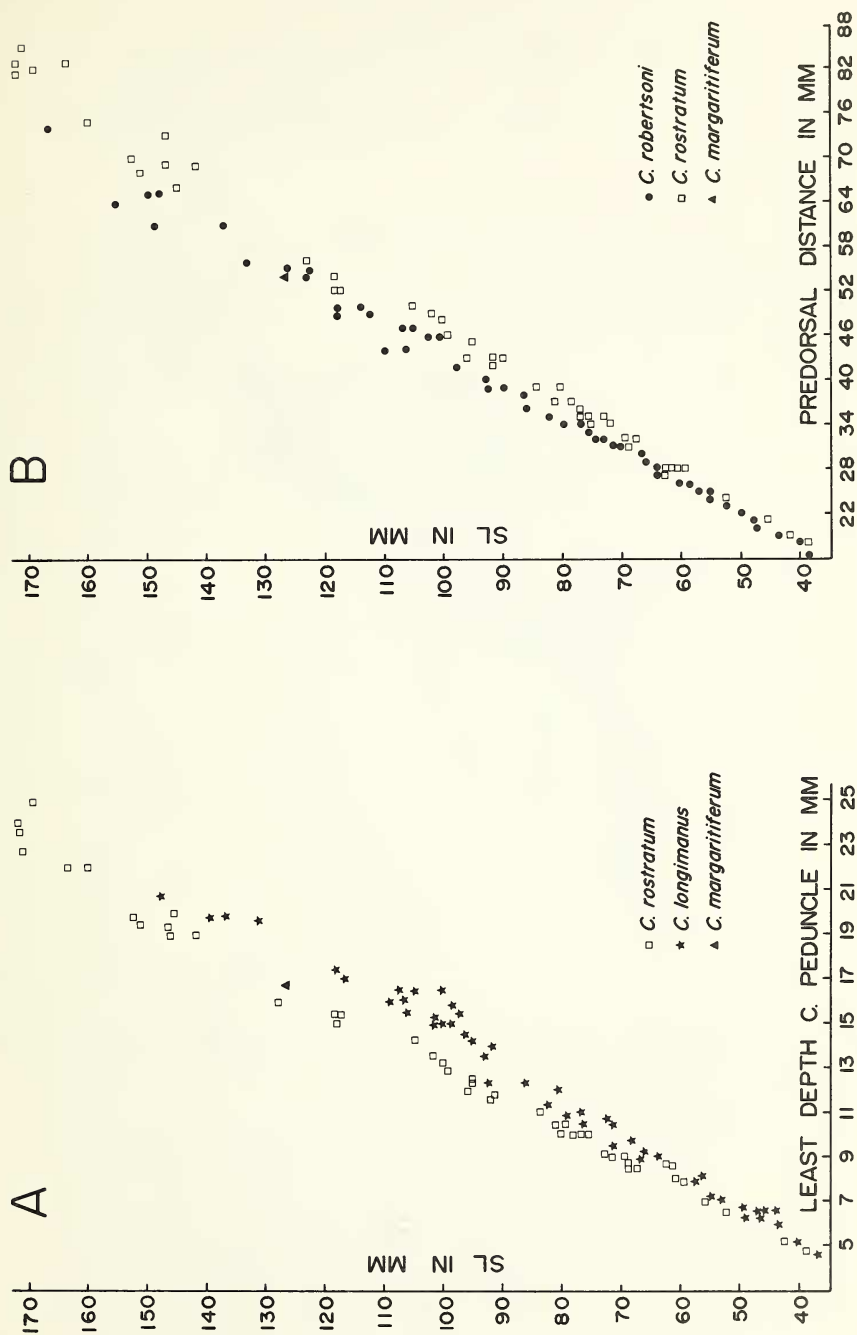
FIGURE 7. Caudal peduncle depth and predorsal distance in four species of *Cichlasoma*.



FIGURE 8. Ranges of *Cichlasoma robertsoni*, *C. longimanus* and *C. rostratum*. *C. longimanus* comprises two allopatric populations: the Lago de Nicaragua population is sympatric with *C. rostratum* in the south and the northern population is replaced by *C. robertsoni* to the north.

sidad de Costa Rica (UCR). Additional material was borrowed or data obtained from the following institutions: British Museum of Natural History (BMNH), California Academy of Sciences (CAS), Museum National d'Histoire Naturelle, Paris (MNHN), University of Michigan, Museum of Zoology (UMMZ) and National Museum of Natural History (USNM).

KEY TO THE SPECIES

Adult coloration is not fully attained until individuals of the species considered below reach 60-70 mm SL. Other characteristics such as shape of caudal margin are only apparent on well-preserved and undamaged juveniles. Thus, although certain characters are of value only in identifying adults, some body markings, such as the vertical bar pattern, are most evident in the young.

- A. Caudal fin truncate or rounded; small distinct black spots on interradi-
al membrane of spinous dorsal fin (Fig. 10c), usually extending onto soft dor-
sal; counting first short bar inclined toward head, 8 or 9 vertical bars on
body; lateral blotch on fifth bar (Fig. 10a); third bar not Y-shaped, although
third and fourth bars may be approximated ventrally; anal fin spines 5-7,
modally 6; color in life olive to dark brown above, white or silvery below;
blue spots often on head, body or fins; dorsal fin not edged with red; Atlantic
slope from Veracruz, Mexico to 50 km E of La Ceiba, Honduras
.....*C. robertsoni*
- AA. Caudal fin slightly emarginate; small black spots on interradi-
al membrane of spinous dorsal usually absent, fin dusky, clear, or with irregular blotches,
soft dorsal with dark and/or pale spots; counting first short bar inclined
toward head, 7 or 8 vertical bars on body; lateral blotch on fourth bar (Fig.
12b); third bar Y-shaped (Fig. 12b); anal fin spines 5-8, modally 7 ... B
- B. Lateral blotch small, scarcely noticeable on fourth vertical bar of trunk; third
and fourth trunk bars very prominent (Fig. 12c); crescentic blotch on
posteroventral margin of opercle; 5 sensory pores on mandible; Guatemala
(known only from type) *C. margaritifera*
- BB. Lateral blotch large, not hidden by vertical bar; trunk bars nearly obsolete in
adults; no opercular blotch; 4 sensory pores on mandible C
- C. Caudal and usually soft dorsal and anal fins entirely covered by small clear
spots on dark background (Fig. 9); no dark lateral band uniting eye with
lateral spot; a diffuse dark lateral band uniting eye with lateral spot; a diffuse
dark "saddle" below 7-11th dorsal spines; pectoral rays 15-17, modally 16;
dorsal rays 10-13, mean 11.7; vertebrae 28-30, modally 29; ground color in
life yellow to yellow-green above, yellow below; random blue spots over
body and median fins of adults; dorsal fin not edged with red; Atlantic slope
from Great Lakes basin, Nicaragua to Río Matina basin, Costa Rica
.....*C. rostratum*

CC. Alternating light and dark areas often producing "checkerboard" effect on soft dorsal fin (Figs. 11 and 12); soft anal and caudal fins with few or no spots, caudal fin at most with a few indistinct clear spots proximally; a dark, sometimes intermittent, lateral band uniting eye with lateral spot; no saddle below dorsal spines; pectoral rays 13-17, modally 15; dorsal rays 9-13, mean 10.2; vertebrae 27-29, modally 28; ground color in life silvery, gray or olive above, throat or lower sides reddish in most populations; blue spots, if present on body, forming regular rows; dorsal fin margin red or orange; Atlantic slope from Río Aguan basin, Honduras to Río San Juan basin, Costa Rica; Pacific slope from Río Colojate, Guatemala to Río Bebedero drainage, Costa Rica *C. longimanus*

Cichlasoma rostratum (Gill and Bransford)

Figure 9

Heros rostratum Gill and Bransford 1877, Acad. Nat. Sci. Philad., Proc. 29:181 (type: Lago de Nicaragua, Nic.).

Taxonomic History

Gill and Bransford (1877) believed *C. rostratum* to be of the "*helleri* type" and most closely allied to *Heros affinis* of Lago Petén, Guatemala. Jordan and Evermann (1989) repeated the original description.

Pellegrin (1904) provisionally included *rostratum* in the synonymy of *Cichlasoma helleri* of his subgenus *Cichlasoma*.

Meek (1904) placed *helleri*, *affinis*, *rostratum* and other species in his new genus *Thorichthys*. Meek (1907) described new material from Lago de Managua and Lago de Nicaragua and suspected (1908) that *rostratum* may be synonymous with *longimanus*. Meek (1914) collected *rostratum* of both sexes in Costa Rica, thus suppressing its proposed identity with *longimanus*.

Regan (1905) redescribed one of the types and later (1906-08) published the first figure of the species and, followed by Eigenmann (1910), assigned it to his Section *Astatheros*.

Jordan, Evermann and Clark (1930) included *rostratum* in *Astatheros* and elevated Pellegrin's subgenus to generic rank.

Description

General.—*C. rostratum* is a moderate to deep-bodied *Cichlasoma* with produced snout, long pectoral fin and emarginate caudal fin. Prominent body markings include a large black blotch above tip of pectoral fin, a small caudal spot and seven vertical bars, which become obsolete with age. Small pale spots cover the dusky caudal and soft dorsal and anal fins and readily distinguish the species from *longimanus*. The mouth is wide and highly protractile. Lips are very fleshy and especially in some river specimens (Figs. 9b and c) the lower lip forms broad lateral folds, which approach those of *C. altifrons*. Large specimens of both sexes have nuchal gibbosities that of the males being larger.

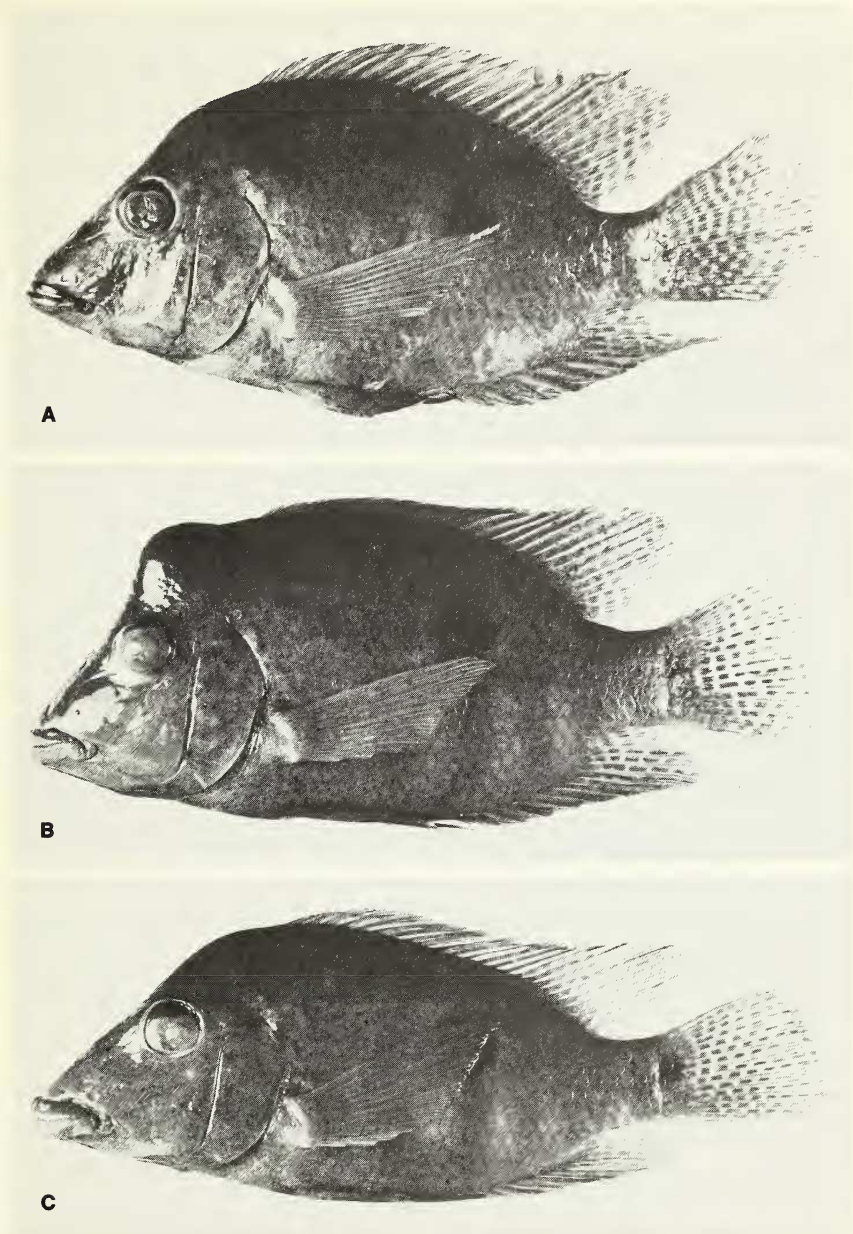


FIGURE 9. *Cichlasoma rostratum* (Gill and Bransford). A. Male, 147 mm SL, from Lago de Nicaragua, UCR 542-1. B. Male, 170 mm SL, from tributary of Lago de Nicaragua, UCR 122-17. C. Female, 147.5 mm SL, from tributary of Lago de Nicaragua, UCR 124-10.

Variation.—No significant physical barriers to a free genetic interchange are known to exist between the Río San Juan basin and rivers of adjacent lowland plains. Thus, not surprisingly, little geographic variation is indicated in meristic counts for *rostratum*. A specimen from Laguna de Masaya, Nicaragua, a crater lake with no outlet, presents average meristic counts.

C. rostratum has either 16 or 17 ($\bar{x}$ = 16.3) dorsal spines. The mode was commonly 16, but in the Río San Carlos drainage the mode was 17 spines. Dorsal soft-rays vary from 10-13 ($\bar{x}$ = 11.7), but most specimens have 11 or 12 rays. Anal spines vary from 6-8 ($\bar{x}$ = 6.9) and most fish have 7 spines. Anal soft-rays vary from 7-9 ($\bar{x}$ = 8.2) and most specimens have 8 rays. Pectoral rays vary from 15-17 ($\bar{x}$ = 16.0) and the mode is also 16.

Gill rakers vary between 17-21 ($\bar{x}$ = 19.3). Most fish have 18-20 gill rakers. Most specimens have 20-21 pores in the upper lateral line. The total range is 16-23 ($\bar{x}$ = 20.0). There is evidence of an increase in pore number from north to south. The number of pores in the lower lateral line is highly variable, 6-13 ($\bar{x}$ = 11.0). Most specimens have 10-12 pores.

Longitudinal scales vary from 26-31 ($\bar{x}$ = 28.2). Most fishes have 27-29 scales. Scales above lateral line vary from 4-6 ($\bar{x}$ = 5.0). Most specimens have 5 scales. Scales around caudal peduncle vary from 15-18 ($\bar{x}$ = 16.2). Vertebrae vary from 28-30; most specimens have 29 (Table 1).

A few salient proportional differences exist between lake and river populations. Lacustrine *rostratum* (Fig. 9a) have shorter and deeper bodies (body depth 1.9-2.2 times in SL, usually 2.0) and their pectoral fins are longer (usually equal to head length vs shorter than head length).

Coloration.—Ground color is yellow or golden brown according to color phase. Nonbreeding individuals are golden brown above becoming golden or yellow overlain with green on sides, breast bright yellow. A diffuse saddle below spinous dorsal fin. An oval black spot lies between the two lateral lines above tip of pectoral fin. A small, vertically elongate black spot lies on upper half of caudal fin base.

Seven indistinct vertical bars cross body. These dark bars are more prominent on juveniles, but may be visible on large adults. The first bar extends from occiput to upper margin of gill opening. The second bar extends from dorsal origin to pectoral axil. The third and most prominent bar is Y-shaped and crosses the body below the fifth to eleventh dorsal spines; the forked part of the Y fills in and becomes a dark saddle in adults. No blotches occur on bars two and three as in *longimanus* and some *robertsoni*. The fourth bar crosses the body below dorsal spines 11-13; an intense black blotch lies on its upper half. The fifth bar commences below first few dorsal soft-rays and the sixth below the last dorsal rays. The seventh bar crosses the middle of caudal peduncle. The width of cross bars is subequal to interspaces. The lateral blotch is subequal to eye diameter in young, but larger than eye, in largest specimens. A smaller irregular spot occurs on middle or slightly above center of caudal fin base.

Antero-lateral scales are bright golden with dusky borders. Small iridescent pale blue spots are scattered irregularly on upper half of body. These spots are

more concentrated around the lateral and caudal blotches, where they form an indistinct ocellus.

The upper head is golden brown, lower cheek and operculum golden and gular region pale tan. The lips are notably dark or black. Small pale blue spots may occur on the operculum and darker blue spots sometimes below the eyes. The iris is golden.

Pectoral fins are transparent. Pelvic fins are dusky yellow. Median fins are dark brown to black with rows of pale blue or clear spots. Clear spots cover the soft dorsal in curved vertical rows. These spots are blue at base of fin and also may extend in one or two rows along lower half of spinous dorsal fin. Dorsal fin not edged in red. Slightly larger round or square spots cover the caudal fin, which often results in a "checkerboard" pattern where the spots are nearly equal in area to the dark interspaces. The soft anal fin is covered distally with transparent spots and proximally with blue spots.

Breeding fish are considerably dusker over the entire body and fins. Ground color is golden brown overlain posteriorly with considerable blue. The bright blue spots contrast strongly with the dark brown dorsum and nearly black median fins. Top and sides of head are dark purplish brown. Lips and throat are black. Pectoral fins are dusky and pelvic fins dark brown.

Young are pale silvery; at 16 mm SL the lateral spot is pronounced, a caudal bar is visible and vertical bars are forming on the body. At 22 mm SL seven vertical bars are apparent. At 34 mm SL the caudal fin has dark streaks and spots alternating with transparent areas. A 45 mm SL specimen has a completely transparent-spotted caudal and soft dorsal and anal fins and very prominent vertical bars. At about 90 mm SL barring fades leaving upper part of Y-shaped bar as a diffuse blotch below middle of spinous dorsal; transparent spots turn blue on soft dorsal, anal and caudal fins; blue spots also begin to appear on dorsum and head.

Sexual dimorphism.—It often is difficult to distinguish sexes externally in *rostratum* without examining the urogenital papilla. Most larger fish are males and the larger member of a breeding pair is a male (Gerald H. Meral, personal communication). Large fish of both sexes present a nuchal hump, although only males have a very prominent hump, which may protrude as much as 15 mm from the normal predorsal profile (Fig. 9b). The general shape of urogenital papillae of both sexes may be slim and pointed or broad and rounded. The firm tip of the male papilla is either smooth and pointed or with projecting membranous filaments; the urogenital opening is not readily apparent. The female papilla terminates in a spongy scalloped border with a large ventral opening.

The maximum size for the species, 185 mm SL (235 mm TL) was attained by a male and female from UCR 264-6. The smallest sexually mature individuals of each sex examined were 100 mm SL.

Juvenile distinctions.—In specimens smaller than 35 mm SL, the black lateral spot (about orbit diameter), produced snout, and diamond-shaped outline (exclusive of fins), distinguish *rostratum* from other sympatric *Cichlasoma*, save *longimanus*. Due to great intraspecific variation in *longimanus*, no one combina-

tion of characters serves to distinguish juveniles of all populations from *rostratum*. Nevertheless, it is possible to distinguish *rostratum* from each *longimanus* population individually. Where they are sympatric in the Great Lakes basin of Nicaragua, *rostratum* has a longer snout, lower profile and less body depth than *longimanus*. Young *rostratum* are distinguished from *robertsoni* by their Y-shaped third cross bar and lateral spot, which is borne on the fourth rather than fifth cross bar.

Distribution and Ecology

C. rostratum is restricted to Atlantic slope drainages of Nicaragua and Costa Rica. The Pacific slope record of *rostratum* (Bussing 1967) refers to specimens of *longimanus*. The known range of *rostratum* includes Lago de Managua, Lago de Nicaragua, Laguna de Masaya and affluents of the Great Lakes basin. Collections from the Río Escondido, to the north have not yielded the species, but the exact northern limit has not been determined for lack of intermediate collections. Meek (1914) obtained the species in Río Zent of the Río Matina drainage and this is the southern known limit. *C. rostratum* never was collected in large numbers, but it is a typical element of lowland tributaries of the Río San Juan. It was taken from near sea level at Tortuguero (Gilbert and Kelso 1971) to 135 m at Laguna de Masaya.

C. rostratum is associated with leaf and detritus bottom in Lago de Nicaragua. During experimental trawling over the northern sector of the lake in 1971 the species was taken only at the mouth of rivers or in other areas where large deposits of terrestrial vegetation had accumulated. The species occurs in rivers with considerable rocky bottom, but it has been observed in areas of slow current, fine sediments and detritus. Adults congregate in pairs near rocks or logs.

The species swallows large mouthfuls of sediment, which are passed out through the gill openings. Roughly 50 percent of the gut contents of *rostratum* of all sizes were aquatic insect larvae. Detritus and silt made up the bulk of the remaining items.

Cichlasoma robertsoni Regan

Figure 10

Cichlasoma margaritiferum, Pellegrin (not Günther) 1904, Soc. Zool. France, Mem. 16:211.

Cichlosoma robertsoni Regan 1905, Ann. Mag. Nat. Hist. Ser. 7, 16:239 (type: Stan Creek, British Honduras).

Cichlasoma acutum Miller 1907, Amer. Mus. Nat. Hist., Bull. 23:117, fig. 6 (type: Río Tenedores, Guat.)

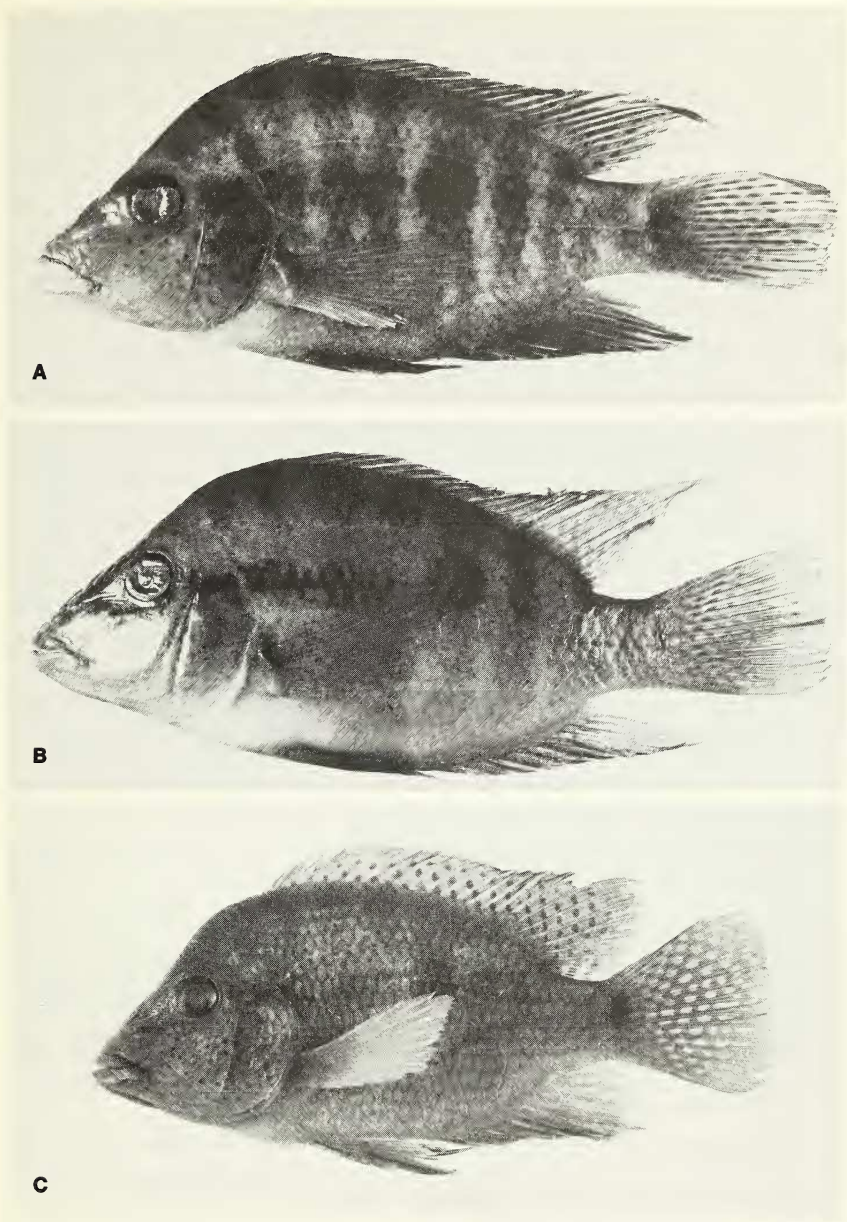


FIGURE 10. *Cichlasoma robertsoni* Regan. A. Female, 117.5 mm SL, from northwestern Honduras (100 m), UCR 517-1. B. Female, 120.5 mm SL, from northern Honduras (10 m), UCR 518-1. C. Specimen, 122 mm SL, from northwestern Honduras (30 m), LACM 32373-3.

Taxonomic History

Pellegrin (1904) assigned several specimens from Guatemala to *Cichlasoma margaritiferum* Günther. Our studies indicate that this material is referable to *C. robertsoni*.

Regan (1906-08) published the first figure, based on the small type specimen, and assigned *robertsoni*, followed by Eigenmann (1910), to his Section *Astatheros*.

Miller (1907) described *C. acutum* from a large series taken in the Río Motagua drainage, Guatemala. Miller (1966) placed it in the synonymy of *robertsoni*.

Jordan, Evermann and Clark (1930) placed *robertsoni* in the genus *Astatheros* and *acutum* in the genus *Thorichthys*.

Description

General.—*C. robertsoni* is a moderate to deep-bodied *Cichlasoma* with produced snout, moderately long pectoral fin, and a truncate or sometimes rounded caudal fin. All specimens have a large lateral blotch above tip of pectoral fin and a small caudal spot, slightly larger than that of *longimanus*. A faint horizontal band joining eye to lateral blotch, as in *longimanus*, is present or absent. Eight or nine dark vertical bars cross body between head and caudal fin. The soft dorsal fin has dark and/or clear spots. Dorsal and anal fins are typically produced into filaments in adults. Lips are normal. All specimens have a rather straight profile from snout tip to just before dorsal origin. Only largest males reveal a slight nuchal gibbosity (Fig. 10c).

Variation.—Dorsal spines vary from 14-17 ($\bar{x}$ = 16.1). Most specimens have 10-12 dorsal soft-rays ($\bar{x}$ = 11.0); the range is 9-13 rays. Population A has a significantly higher mean ($\bar{x}$ = 11.4) than Population B ($\bar{x}$ = 10.8).

Anal spines vary from 5-7 ($\bar{x}$ = 6.1), but most specimens have 6 or 7 spines. Population A has a mean of 5.9 and only 2 percent of individuals with 7 spines. Population B has a significantly higher mean ($\bar{x}$ = 6.2) and 21 percent of the population with 7 spines. Most specimens have 7-9 anal soft-rays ($\bar{x}$ = 8.6), but two specimens from Population A and one from Río Motagua, Guatemala have 10 anal soft-rays. Pectoral rays vary from 14-16 ($\bar{x}$ = 15.0) and the mode also is 15.

Gill rakers vary between 15-20 ($\bar{x}$ = 17.6), but most specimens have 17 or 18 gill rakers. Population A has a significantly higher count ($\bar{x}$ = 18.3) than Population B ($\bar{x}$ = 17.3).

The number of pores in the upper lateral line is quite variable, 18-24 ($\bar{x}$ = 20.3). Population A has a significantly higher mean ($\bar{x}$ = 20.9) than Population B ($\bar{x}$ = 20.0). The number of pores in the lower lateral line is also variable with a range of 7-13 ($\bar{x}$ = 10.1). Most specimens have 9-12 pores. The Honduran populations have 10 or 11 ($\bar{x}$ = 10.8) with 2 specimens with 13 lower lateral line pores and one specimen with 7 lower lateral line pores.

Most specimens have 27-29 longitudinal scales and a range of 25-31 ($\bar{x}$ = 28.2) scales for all populations.

Scales above the lateral line vary from 5-7 ($\bar{x}$ = 6.1), the mode is six. Population B has a significantly higher mean ($\bar{x}$ = 6.2) than Population A ($\bar{x}$ = 5.9).

Scales around the caudal peduncle vary from 16-20 ($\bar{x}$ = 18.2). Most specimens have 18 or 19 scales. Vertebrae vary from 29-30, the mode is 29 (Table 1).

Despite its large range, and unlike *longimanus*, *robertsoni* exhibits little morphometric variation. Orbit diameter, dorsal spine length, head length, body depth and pectoral fin length show little intraspecific variation in the specimens examined.

Coloration.—Ground color is dark brown to dark olive above. Dorsum is uniformly dark olive brown. Below lateral blotch, the lower sides are silvery white or gray. The belly is white, becoming dusky at pelvic fin base. A black lateral blotch lies between the upper and lower lateral line series, above or distal to the tip of the pectoral fin. A small, vertically elongate basicaudal blotch lies mostly above the lower lateral line. A series of black blotches, formed by the broadened and intensified central portion of the second, third and fourth vertical bars (Fig. 10a), or a black band (Fig. 10b), connecting eye to lateral blotch is typical of some fishes in Population B. This dark humeral band is lacking in specimens from Population A.

Eight or nine dark vertical bars of about equal intensity cross the body. Bars are apparent on most large specimens, but in some populations, are evident only as dorsal blotches or only visible posterior to lateral blotch. A short inclined bar over the eye and an interorbital bar are visible on some adults and young. The first body bar originates at the occiput and intersects the second bar at its midpoint. The second bar (first complete bar) is nearly vertical or inclines forward dorsally; it extends from dorsal spines 1-3 or 2-4 to pectoral axil. The third bar crosses the body below dorsal spines 5-7 or 6-8. The fourth bar lies below dorsal spines 9-11. Bars three and four are more closely approximated ventrally than other bars and are occasionally joined below the humeral band to form a single Y-shaped bar. The resultant bar can be distinguished from the Y-shaped third bar of *longimanus* and *rostratum* by its much wider ventral half. The fifth bar bears the lateral blotch on its upper half and lies below dorsal spines 12-14 or 13-15. Bar six crosses the body below the first three dorsal soft rays. Bar seven lies below the end of soft dorsal. An additional bar (eighth) may or may not lie closely behind bar seven. The last (eighth or ninth) bar crosses the caudal peduncle. Bars are always wider than interspaces.

Scales above the lower lateral line are generally smaller than scales below.

The antero-lateral body scales are iridescent silver and have little of the bluish white or pearl coloration of the scales of *margaritiferum* and some *longimanus*.

The upper head, cheeks and operculum are dark yellow-brown to olive. On specimens with a humeral band, an extension of this band lies on the upper operculum behind the eye. Iridescent blue spots or vermiculations are most common in populations from the Río Ulua drainage, Honduras and British Honduras. Upper jaw and snout are olive brown to brown. The lower lip is white or cream to gray. The iris is iridescent yellow to gold.

Pectoral fins are uniformly light brown to light yellow. Juveniles have clear

or dusky pectoral fins. Pelvic fins of adults have melanophores along first two fin elements, giving a dark or black appearance when the fin is retracted. Juveniles and some adults have pale pelvic fins with little or no pigmentation. Pelvic soft rays are pale or dusky.

The spinous dorsal fin is pale to dusky with small round or oval spots on the interradi al membranes of most specimens. Dark blue or black spots typically cover the soft dorsal fin and are usually continuous with spotting on the spinous dorsal fin. In the population near El Progreso, Honduras (Fig. 10c), spotting is mainly restricted to the basal half of spinous dorsal. The dorsal fin is not edged with red as in *longimanus*. Round or rectangular clear spots cover the caudal fin, but contrast less than those of *rostratum*. The soft-anal fin is covered posteriorly with black or blue spots.

Young are pale silver with a white abdomen. The vertical bar pattern is far less distinct than in juvenile *longimanus* or *rostratum*. At 20 mm SL, the lateral spot is evident, though within the margins of the fifth vertical bar. It is approximately $3/4$ the eye diameter. The elongate caudal marking is present, as are eight body bars, which extend onto the dorsal fin. The paired fins are transparent. Dorsal, anal, and caudal fins have dark streaks and mottling. At 25 mm SL, the caudal fin has horizontal dark streaks and alternate clear areas. At 30 mm SL, the soft-dorsal fin has dark spots on a clear background. On juvenile specimens less than 50 mm SL, the Y-shaped appearance of bars three and four is not conspicuous as is the Y-shaped third bar of *rostratum* and *longimanus*. At 45 mm SL, fin spotting, body pattern and coloration is that of an adult. From 35 to 50 mm SL, the body bars tend to fade on some fish. At 70 mm SL, spotting on the soft dorsal and anal fins becomes distinctive. The interradi al membranes of the spinous dorsal and anal fins become uniformly dusky to gray on fish from 35 to 70 mm SL.

Sexual dimorphism.—There appears to be little correlation between body size and sex, although most fish greater than 140 mm SL are males. The sex ratios for both Population A and B is almost two males to one female. The male urogenital papilla is conical and sometimes with a pointed tip. The opening of the papilla is terminal; the tip is bifurcate and has short filaments or palps on large males. The larger member of a breeding pair is generally a male (LACM 32435-5).

The female papilla is broader and shorter than that of the male and terminates in a flattened, broadened structure with a ventral opening. As with other *Amphilophus* species, the ventral surface of the female urogenital papilla does not extend to the tip of the structure, but forms a broad ventral opening with a scalloped anterior margin.

The maximum size for the species is a 166 mm SL male from the Río Sarstun, Guatemala (USNM 114354). Specimens greater than 125 mm SL are uncommon in collections.

Juvenile distinctions.—In specimens less than 40 mm SL, the large lateral blotch, the greatly produced snout, and the deep body distinguish *robertsoni* from other sympatric *Cichlasoma*, except members of the *Thorichthys* species group. In areas of sympatry with *Thorichthys* group species, *robertsoni* lacks the

characteristic subopercular blotch, and the intense, prominent blue head spotting of *Thorichthys* representatives (especially *C. aureum*). The absence of a conspicuous Y-shaped bar before the lateral spot and the presence of the lateral spot on the fifth rather than fourth cross bar distinguish *robertsoni* young from *longimanus* and *rostratum*.

Distribution and Ecology

C. robertsoni is restricted to the Atlantic lowlands of Central America, from the Río Coatzacoalcos drainage, Veracruz, Mexico to the independent tributaries of the Departamento de Colón, Honduras (Fig. 8). The known range of *robertsoni* includes Lago Petén, the major lakes and streams of Atlantic Guatemala, British Honduras, and southern Mexico. It is distinctively absent from collections on the Yucatán platform, Mexico. It occurs from sea level to a maximum elevation of 160 m in Río Ulua, Honduras.

C. robertsoni is predominately a sluggish river or backwater associated species. It is common in areas of high accumulation of leaf detritus and from clear to highly turbid water. It occurs most frequently over silt-mud substrate, but at higher elevation inhabits rocky streams. Associated vegetation included filamentous green algae (*Spirogyra*), attached green algae (*Chara*), water weed (*Elodea*) and sedges (*Carex*) along the stream margins. Adults tended to aggregate in pairs among rocks or logs. Juveniles (generally less than 50 mm SL) frequently inhabited shallow areas or tributaries to rivers. The species was collected at water temperatures ranging from 21-31° C in Honduras.

Cichlasoma longimanus (Günther)

Figures 11 and 12

Heros longimanus Günther 1868, Zool. Soc. Lond., Trans. 6:453, pl. 72, fig. 2 (type: Lago de Nicaragua, Nic.).

Cichlasoma popenoei Carr and Giovannoli 1950, Mus. Zool., Mich., Occ. Papers 523:31, pl. 2, fig. 2 (type: Río Yeguaré, Honduras).

Taxonomic History

Günther (1868) described *Heros longimanus* from a single specimen taken by Captain Dow in Lago de Nicaragua, and likened it to the Mexican *Heros helleri*.

Pellegrin (1904) gave a brief synopsis and a few more meristic counts, and included it in his subgenus *Cichlasoma*.

Meek (1904) proposed a new genus, *Thorichthys*, to include *helleri*, *longimanus*, *rostratum* and others. Meek (1908), who had limited adult material, suggested that *longimanus* may represent females of *rostratum*. Later, Meek (1914) retracted his proposal on discovering *rostratum* of both sexes in Costa Rica. Astorqui (1972) also commented on the difficulty of distinguishing young preserved *longimanus* from *rostratum*.

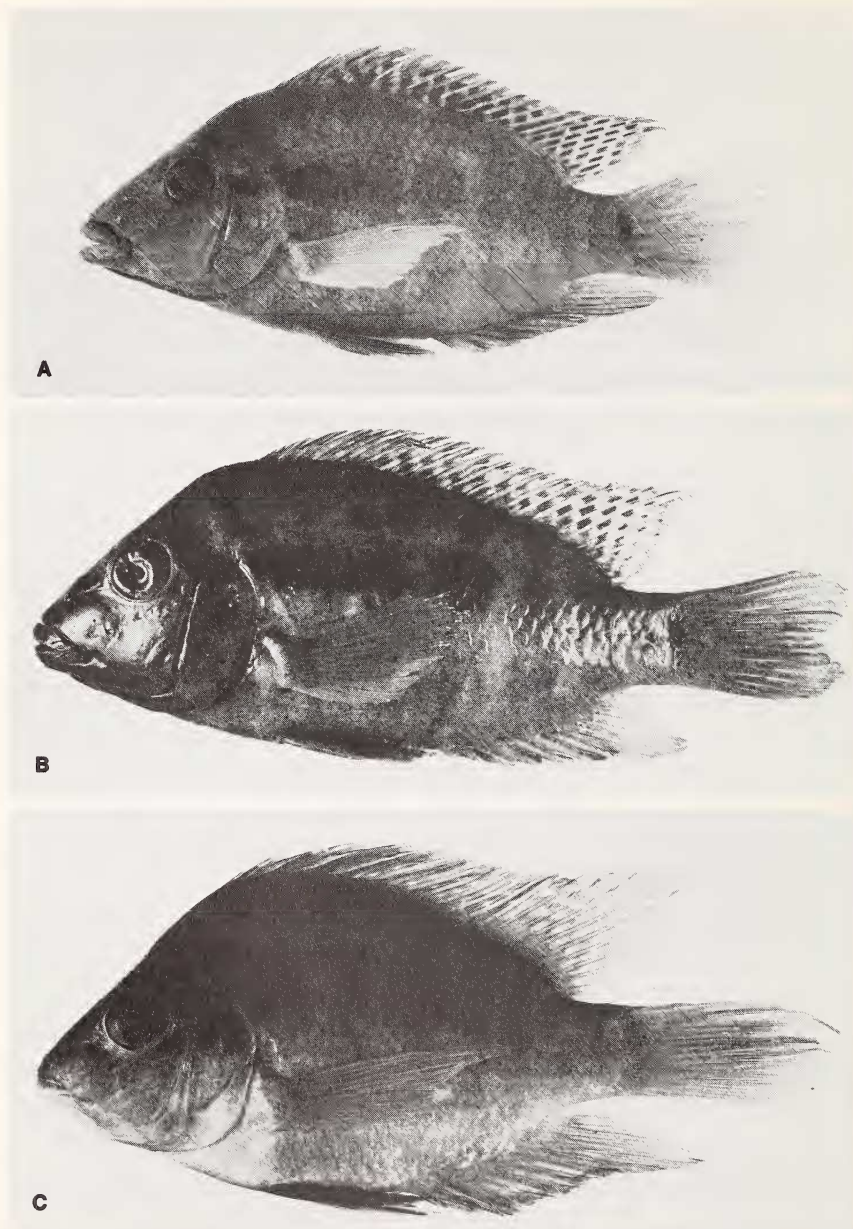


FIGURE 11. *Cichlasoma longimanus* (Günther) from Atlantic versant. A. Specimen, 108 mm SL, from northeastern Honduras (470 m), LACM 32313-4. B. Female, 112 mm SL, from Río Coco drainage, Nicaragua (700 m), UCR 473-1. C. Male, 99 mm SL, from Lago de Nicaragua, UCR 24-6.

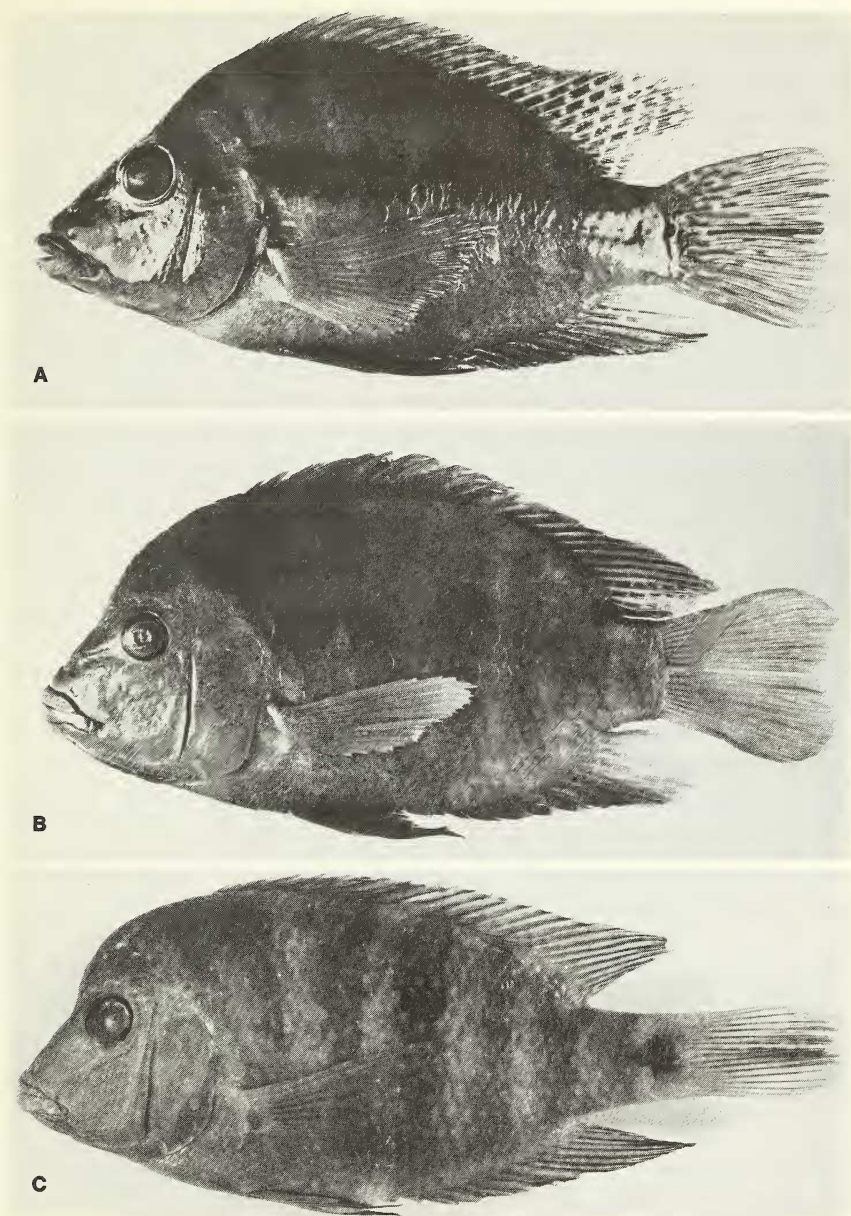


FIGURE 12. *Cichlasoma longimanus* (Günther) from Pacific versant. A. Male, 109 mm SL, from El Salvador, UCR 316-5. B. Male, 121 mm SL, from Finca Taboga, Costa Rica, UCR 153-1. *Cichlasoma margaritiferum* (Günther). C. Holotype, 126.7 mm SL, from Guatemala, BMNH 1864-1-26-62.

Regan (1905) redescribed the type and, followed by Eigenmann (1910), included the species in his Section *Astatheros* (1906-08).

Jordan, Evermann and Clark (1930) elevated Pellegrin's *Astatheros* to genus to include *longimanus*.

Carr and Giovannoli (1950) were first to describe a Pacific slope population of *longimanus*. They named the species *Cichlasoma popenoei* and based it on 36 specimens from the Río Choluteca drainage, Honduras. They referred *popenoei* to Section *Astatheros* (*Amphilophus*) and considered it most closely related to *rostratum*. No comparison was made with *longimanus*.

C. longimanus, perhaps due to its disjunct and curious distribution pattern, is an exceptionally variable cichlid with respect to general body form and details of color pattern. One Population (F) is apparently allopatric and has adapted to the Great Lakes basin of Nicaragua and northern Costa Rica. The other Populations resemble in distribution a modified H, which straddles the continental divide of Central America: an Atlantic Population (C) in Honduras and northern Nicaragua, which unites with Pacific slope populations through the highlands of Honduras; Population D constitutes the northern Pacific branch and Population E the southern Pacific segment. At the southern extreme of Population E a distinctive variant population is somehow maintained in part of the Río Bebedero drainage.

Description

General.—*C. longimanus* is a moderate to deep-bodied *Cichlasoma* with produced snout, moderate to exceptionally long pectoral fin, dorsal spines very short to very long and emarginate caudal fin. All specimens present a large lateral blotch above tip of pectoral fin, a small caudal spot and a horizontal band joining eye to lateral blotch. Seven or eight dark vertical bars cross the body between head and tail. The soft dorsal fin has clear and/or dark spots. Other fins are generally unspotted. The mouth is not as wide, nor the lips as fleshy as in some *rostratum*. Largest males have a slightly more convex nuchal profile, but no gibbosity as in *rostratum*.

Meristic variation.—Dorsal spines vary from 14-17 ($\bar{x}$ = 16.1); the mean counts vary only slightly from population to population. One specimen from Atlantic Costa Rica has the lowest spine count (14). Most specimens have 9-11 dorsal soft-rays ($\bar{x}$ = 10.2), but specimens from Atlantic Costa Rica exhibit the full range of 9-13 rays. Specimens from Population E have a significantly lower count ($\bar{x}$ = 9.9) than other Populations.

Anal spines vary from 5-8 ($\bar{x}$ = 7.0). Most specimens have 6-8 spines, but one specimen from Population C has 5 anal spines. All specimens have 7-9 ($\bar{x}$ = 8.0) anal soft-rays. Examples from Population E have a significantly lower count ($\bar{x}$ = 7.7) than other Populations.

Pectoral rays vary from 13-17. Most specimens have 14-16 ($\bar{x}$ = 15.1) rays. Population E has a significantly lower count ($\bar{x}$ = 14.9) than other Populations and one specimen (Pacific Costa Rica) with 13 rays. Two specimens from Atlantic Costa Rica have 17 rays.

Gill rakers vary from 15-20 ($\bar{x}$ = 17.5). Population F has a significantly higher count ($\bar{x}$ = 18.4) than other Populations and is the only Population with counts of 20 gill rakers.

Although most specimens have 18-22 pores in the upper lateral line, the full range is 16-26 ($\bar{x}$ = 20.0). Pacific Populations D and E have one specimen with 24 and two specimens with 26 pores, although their means are not significantly greater than other Populations.

The number of pores in the lower lateral line varies from 7-12 ($\bar{x}$ = 10.0). Population F has a significantly lower count ($\bar{x}$ = 9.6) than other Populations and three specimens with 7 pores.

Most specimens have 27-29 longitudinal scales, but the extreme variation recorded is 25-32 ($\bar{x}$ = 27.7). Population E has a significantly higher count ($\bar{x}$ = 28.3) and two specimens with 31, and one specimen with 32 longitudinal scales.

Most specimens from Populations D, E and F have 5-6 ($\bar{x}$ = 5.6) scales above lateral line, but counts of 7 are common in Population C. The mean count for Population C ($\bar{x}$ = 6.3) is significantly greater, and for Population F ($\bar{x}$ = 5.0) significantly less, than Populations D and E.

Scales around caudal peduncle vary from 16-21 ($\bar{x}$ = 1.8). Specimens from Population E have a significantly higher count ($\bar{x}$ = 19.0) including several individuals with counts of 20 and two specimens with 21 scales. Population F has a significantly lower count ($\bar{x}$ = 16.9) than other Populations. Vertebrae vary from 27-29, most specimens have 28 (Table 1).

Morphometric variation.—Certain proportions are valuable in distinguishing local populations of *C. longimanus* (specimens >70 mm SL): head length /length of sixth dorsal spine, head length /orbit diameter, standard length/greatest body depth, pectoral fin extension and angle and contour of dorsal profile.

The sixth dorsal spine length is contained 1.9-3.7 times in head length. In most specimens from Populations C and D the proportion is 2.1-3.2. The sixth spine is shorter in Population E (2.5-3.7), with the extreme of 3.7 found only at Finca Taboga in the Río Bebedero drainage of Costa Rica. Longer spines (1.9-2.7) are typical of Population F, with the longest spines (1.9 in head) found in the population from Lago de Nicaragua (Fig. 11c).

The orbit diameter is contained 3.5-5.1 times in head length. Specimens from Populations C, D and F have larger orbits (1.9-3.2) with respect to head length than Population E fishes (4.0-5.1). Finca Taboga specimens had the smallest orbit diameter (4.8-5.1) of any population (arrows in Fig. 4b). When orbit diameter is plotted against SL on a scatter graph, specimens from Population F usually can be distinguished from Populations C, D and E by their larger orbits (Fig. 4b).

Body depth is not as definitive a measurement as others, but is useful in describing certain populations. Body depth is contained 1.8-2.5 times in SL. Most specimens from Populations C, D and E have proportions of 2.1-2.5, except the deep-bodied Finca Taboga material (1.9-2.0). Specimens from Population F also have a greater body depth (1.8-2.2) than other Populations.

The longer caudal fin of specimens in Population F is of some value in distinguishing them from Populations C, D and E (Fig. 5b).

The pectoral fin reaches to the third to sixth anal spine of most specimens. The Finca Taboga population, however, has a consistently short pectoral, which reaches only to the second or third anal spine (Fig. 12b). Specimens from Lago de Nicaragua have a long pectoral fin, which may extend to the first anal soft ray (Fig. 11c).

Specimens from most populations have a steep, straight dorsal profile from snout tip to near dorsal fin origin, where it describes a gradual curve along the back. Examples from the Río Prinzapolka drainage, Nicaragua are notable for their straight, but lower profile, which begins to curve well before the dorsal origin. Large specimens from Finca Taboga, Costa Rica have a slight nuchal gibbosity, which produces a concave profile above the eyes (Fig. 12b). Specimens from Laguna de Xiloá, Nicaragua often have a distinctive convex dorsal profile.

Coloration.—Ground color is dark olive-brown or grey above. Below the lateral blotch, sides are abruptly silvery white. Lower sides, particularly anteriorly, are suffused with pink or rose color in many populations. Belly is white, but dusky around pelvic base. A black lateral blotch, subequal to orbit diameter, lies above or anterior to tip of pectoral fin. A series of discontinuous black blotches or squares, or a solid black band connects eye to lateral blotch. In some specimens this humeral marking forms a continuous black band, in others it clearly is formed, in large part, by the broadened and intensified central portion of second and third vertical bars. A small, often irregular, spot or vertical bar lies mostly on upper half of caudal fin base; in no case does it cross entire caudal peduncle.

Seven or eight dark vertical bars of about equal intensity cross body. Atlantic slope populations tend to have seven bars, but Pacific specimens usually have eight. Bars become diffuse on large specimens, where they may remain only as blotches along the dorsal fin base. On juveniles or occasional large specimens, a short inclined bar lies over the eyes. This and an interorbital bar are conspicuous on live individuals, but usually visible only on small preserved material. The first bar extends from occiput to posterior edge of gill opening or into axil of pectoral fin. This bar is strongly inclined over the head and often joined to second bar near its midpoint. The second bar (first complete bar) inclines anteriorly on its upper portion and extends from dorsal spines 1-4 to pectoral axil and sometimes onto lower side. Bar three is nearly vertical and always Y-shaped; the Y is nearly bifurcated to the base on a few individuals from the Río Tempisque drainage. It crosses the body below dorsal spines 5-11. The fourth bar, with the lateral blotch on its upper half, lies below dorsal spines 12-14. The three or four remaining bars cross the body between the soft dorsal and soft anal rays and the caudal peduncle. Bars are wider than interspaces anteriorly, but nearly equal behind. The caudal spot is not included in this count.

Upper body scales often reflect a blue iridescence, forming regular rows of blue spots. Small blue spots may irregularly ring the black humeral band and lateral blotch.

The upper head is dark, similar to dorsum; cheek and operculum are golden tan and gular region white or dusky, sometimes suffused with rose. A dark band

usually lies behind eye and is continuous with humeral band. The lower lip is white or cream, the upper lip darker. Iridescent blue spots or vermiculations may be scattered irregularly on side of head. The iris is golden or orange.

Pectoral fins are pale yellow or dusky green. Juveniles usually have clear or white pelvic fins. Some adults have pale pelvics with dusky distal halves, others have completely dark or black pelvic fins. The tip of first pelvic soft ray may be white or dark and prolonged into a filament.

The spinous dorsal fin is pale or dusky, generally with darker mottlings. Some populations present bold black markings on the spinous dorsal; in some Pacific slope populations the barring effect so evident on the soft dorsal fin is repeated (Carr and Giovannoli 1950). In others (Río Prinzapolka drainage), the blotches on spinous dorsal appear to be extensions of the trunk bars. In one specimen from the Río Coco highlands (Fig. 11b), small black spots continue onto the spinous dorsal fin similar to the typical pattern of *robertsoni*.

The soft dorsal fin is inevitably spotted (Figs. 11 and 12); pearl or blue areas (clear in preserved material) alternate with dark or black areas to produce a "checkerboard" effect. The pattern may be produced by pale spots on a dark background, dark spots on a pale background, or pale and black spots on a dusky background. Some spotting is nearly always present on the soft anal fin and occasionally on the basal half of the caudal fin. Specimens from the Honduran uplands have a striking red border to the entire dorsal fin; iridescent blue spots in rows on sides, and head and pinkish lower sides. Coloration is subdued in the Atlantic Honduran lowland; the dorsal margin is orange or yellow and blue spots on head and body are uncommon. Río Prinzapolka fishes taken at 350 m compare well with the Honduran upland specimens. Fishes from Lago de Nicaragua are silvery gray with bright pink lower sides; blue spots are restricted to the area around the black humeral band, and the dorsal fin is edged in orange. Specimens from Pacific Costa Rica are brown above, with yellow-green sides, pale pink on lower sides and isthmus and dorsal fin with thin red border.

Young are silvery with white bellies. At 21 mm SL the lateral spot, slightly smaller than eye diameter, is prominent; a spot is discernible on upper base of caudal fin; a head bar and body bars contrast with pale ground color; all fins, but pectoral, dusky, dorsal fin mottled or not. At 32 mm SL the caudal spot is more defined and body bars begin to pale on some fish. Spotting is visible on soft dorsal and caudal of a 40 mm specimen. At 50 mm SL fin spotting and body pattern is adult.

Sexual dimorphism.—The largest specimens examined were males. Large males from Lago de Nicaragua usually are slimmer than females, but this could not be shown for Atlantic Costa Rican specimens, nor other populations. The male urogenital papilla may be conical or tubular, but always has a narrow or pointed tip. The tip is split on the ventral surface, although the opening is essentially terminal; short filaments often protrude beyond tip. The female papilla is short and conical with a broad rounded or crenulated tip formed by the dorsal half of the papilla. The ventral surface does not reach the tip of papilla, but forms a broad ventral opening ringed by spongy tissue. The shape and structure seem

consistently distinct between sexes except in some specimens from Lago de Nicaragua. Two adult females (UCR 538-1) with well-developed ova had typical male urogenital papillae. The implications of this observation have not been pursued.

Carr and Giovannoli (1950) reported a maximum length of 180 mm SL for *C. popenoei*. Specimens over 110 mm SL are exceptional from other parts of the range. Ripe specimens of only 60 mm SL were examined.

Juvenile distinctions.—The large lateral blotch, produced snout and deep body distinguish *longimanus* from other sympatric *Cichlasoma*, except *rostratum*. In the Great Lakes basin of Nicaragua where the two are sympatric, *longimanus* has a shorter snout, steeper profile and deeper body than *rostratum*. Small *longimanus* are distinguished from *robertsoni* by their Y-shaped third cross bar and fourth cross bar with lateral spot.

Distribution and Ecology

C. longimanus is known on the Atlantic slope of Central America, from the Río Aguan drainage, Honduras to the Río Prinzapolka drainage in northern Nicaragua. In the Great Lakes basin in southern Nicaragua a disjunct population roughly overlaps the distribution of *rostratum*. On the Pacific slope it is known from Arroyo Agua Caliente of the Río Nahualate drainage, Guatemala to the Río Bebedero drainage, Costa Rica. The infrequent and widely separated collections of *longimanus* from the Pacific slope probably reflect the paucity of collecting from the area rather than a discontinuous distribution. In regions of depauperate ichthyofauna, such as the Pacific versant and northern Nicaragua, *longimanus* often occurs in large numbers. It also seems to be one of the more numerous cichlids in Lago de Nicaragua. It was collected between 10 and 850 m elevation.

Adult *longimanus* found in shallow, stagnant drainage canals near Finca Taboga, Costa Rica are darker and more robust than other populations (Fig. 12b). Their proportional peculiarities are described above, although their meristics lie well within the normal variation of the species. A neighboring river population 15 km to the north in the same drainage (UCR 13-7 and 135-7) is distinct in outward appearance, but has the same morphometric tendencies to a lesser degree than Finca Taboga specimens.

C. longimanus occurs in a variety of habitats. Where competition from other cichlids is low, it inhabits main river channels, frequently resisting considerable current. Where *longimanus* and *rostratum* are sympatric, they are ecologically separated. The former occurs in warm, muddy backwaters low in oxygen, while *rostratum* is usually found in running water. Once, however, large numbers of *rostratum* were encountered in a stagnant pool and no *longimanus* were present on this occasion. In Lago de Nicaragua, *longimanus* is found to some extent over all substrates, but is most abundant over soft mud bottom. Gerald H. Meral (personal communication) observed in Laguna de Xiloá that they frequently rest on the bottom and when feeding, take in mouthfuls of sand and chew and spit them out.

Cichlasoma margaritiferum (Günther)

Figure 12 c

Heros margaritifer Günther 1862, Cat. Fishes Brit. Mus. 4:287 (type: probably Atlantic slope, Guatemala or British Honduras).

This enigmatic species is known from a single specimen whose exact type locality is uncertain, although it is probably from the Atlantic slope of Guatemala. Additional specimens of *C. margaritiferum* reported by Pellegrin (1904) are referable to *C. robertsoni*. Two other species have been erroneously synonymized with *margaritiferum*.

Taxonomic History

The original description published by Günther (1862) was repeated by Günther (1868:450, pl. 71, fig. 2) and by Jordan and Evermann (1898).

Kner and Steindachner (1865) remarked on the similarity of *Heros altifrons* to *H. margaritifer* with special reference to the pearl-colored spots covering the body. This is a striking feature in living *altifrons*, and also occurs in some populations of *longimanus*. Many differences, however, clearly distinguish *altifrons* from *margaritiferum*.

Günther (1868) considered that the form described by Steindachner (1864) as *Heros melanopogon*, could represent the young of *margaritiferum*.

Pellegrin (1904) erroneously redescribed *margaritiferum* on the basis of 11 specimens of the then undescribed *robertsoni* from Guatemala, and formally placed *H. melanopogon* in its synonymy. He assigned *margaritiferum* to his subgenus *Cichlasoma*.

Regan (1905) redescribed the type and in 1906-08 included *margaritiferum* in his Section *Astatheros*, a taxon originally proposed by Pellegrin (1904) as a subgenus to include only *Heros heterodontus*.

Eigenmann (1910) assigned *margaritiferum* to the *Erythrichthys* species group, a subgeneric name created by Meek (1907) for a complex of Nicaraguan species.

Jordan, Evermann and Clark (1930) elevated Pellegrin's *Astatheros* to generic rank to include *margaritiferum* and noted that if *Heros labiatum* and *Heros lobochilus* were included in *Astatheros* as Regan had done, then the name *Amphilophus* Agassiz has priority. They also followed Pellegrin in allocating *H. melanopogon* to the synonymy of *margaritiferum*.

As stated above, Günther (1868) suspected that *Heros melanopogon*, described from "Central Amerika" by Steindachner, represented the young of *margaritiferum*. Pellegrin (1904) and Jordan, Evermann and Clark (1930) formally treated *melanopogon* as a synonym of *margaritiferum*.

Regan (1905), repeated by Eigenmann (1910), placed *C. melanopogon* in the synonymy of *Cichlasoma melanurum*, described from Lago Petén by Günther (1862), and assigned *melanurum* to the Section *Theraps*; he also mentioned this synonymy under the species heading of *Cichlasoma gadovii* (Regan 1906-08). He did not comment on Günther's belief or Pellegrin's synonymy.

Hubbs (1935) described *Cichlasoma synspilum* from the Departamento de Petén, Guatemala and considered it closely related to *Cichlasoma maculicauda* Regan. In an addendum he indicated that he had collected additional specimens of *synspilum* and had determined that it is a close relative of *C. melanurum*. Miller (1966) stated that *synspilum* may not be distinct from *melanurum*.

On the basis of our data of *margaritiferum* and the literature, we concur with Regan that *margaritiferum* is referable to Section *Astatheros* (= *Amphilophus*) and is distinct from *C. melanurum* (= *melanopogon*; = *synpilum*?). Section *Theraps*. *C. melanurum* differs from *margaritiferum* in having a rounded caudal fin, very different color pattern and other features.

Redescription of Holotype

General.—*C. margaritiferum* is a deep-bodied *Cichlasoma* with produced snout, gibbous forehead, and emarginate caudal fin. The vertical bar pattern is prominent on the trunk in spite of the large size of specimen. No conspicuous lateral spot above the tip of pectoral fin is present, although the fourth vertical bar is especially intense in the area usually occupied by such a spot. It is significant that no lateral spot was mentioned in the original description. An irregular spot lies mostly on the base of caudal fin. Each scale on side of body has a white pearllike spot. Pale spots cover entire caudal fin, but contrast is slight with the dusky ground color. A few pale spots appear on soft anal and slight mottling on soft dorsal fin. Lips are normal.

Meristics.—The following counts and measurements (mm) were made by Carl L. Hubbs and Laura C. Hubbs on the type specimen (BMNH 1864-1-26-62). D. XVII, 11; A. VII, 9; P₁. 15, 15; P₂. 1, 5 and 1, 5; C. 16; pores in upper lateral line 18, 20; pores in lower lateral line 7, 10; scales above lateral line 6, 7; scales below lateral line 12; oblique scale rows on cheek 5.

Measurements.—Standard length 126.7, head length 43.5, head width 21.7, eye length 8.95, snout length 21.45, upper jaw length 13.85, interorbital width 14.85, least bony interorbital width 14.4, body depth 60.7, least depth caudal peduncle 17.66, caudal peduncle length 18.6, predorsal length 54.2, length longest pectoral fin element 39.8, length longest pelvic fin element 35.6, highest D spine 19.6, highest A spine 19.65, length of A base 38.9.

Additional data were provided by P.H. Greenwood (BMHN), Richard McGinnis (Pacific Lutheran University) and H. Geoffrey Moser (National Marine Fisheries Service, La Jolla). Total gill rakers including rudiments 15; longitudinal scales 30, 31 (3 additional pore-bearing scales on caudal fin base); scales around caudal peduncle 17; diameter of fleshy orbit 10.0; greatest width suborbital 17.0; preanal distance 78.9; prepectoral distance 44.2; prepelvic distance 35.6; length of D base 76.1; caudal fin length 38.0; length of sixth D spine 15.0; length of last D spine 18.1.

Coloration.—Ground color is light brown. Upper and lower sides paler than midsides. A rather large irregular spot lies on basicaudal scales and extends slightly onto caudal peduncle.

Seven vertical bars cross the body, the third and fourth are most intense (Fig. 12c). The first bar extends from occiput to behind upper margin of gill opening. The second bar extends from dorsal origin (dorsal spines 1-5) to just posterior to pectoral axil. The third bar crosses the body below dorsal spines 7-11; it is widest at dorsal base, narrows at midtrunk and widens slightly at its termination above and forward of vent. The fourth and widest bar starts below dorsal spines 12-15, narrows slightly at midtrunk, and reaches origin of anal fin. The fifth arises below dorsal spines 17-19 and drops to last three anal spines. The sixth arises below last six dorsal soft-rays and crosses to last six anal rays. The seventh bar is pale and crosses the entire caudal peduncle at mid-peduncle. There is a dark region on bar four between the two lateral lines and a corresponding (but paler) region on fifth and sixth bars.

Trunk scales each have a pearl white center and are especially apparent on the black cross bars.

The head is brown. A short broad bar lies over the eye and another on the interorbital space. The region behind the eye is paler than surrounding areas. A crescent shaped dark blotch lies on the postero-ventral margin of opercle. P. H. Greenwood (personal communication) described the blotch as "... an attenuated tear drop superimposed on a basically crescentic background. The intensity of the melanic pigment forming the spot is a little less than that of the vertical bars on the flanks, but the spot is quite distinct. It occurs on both sides of the fish and occupies the same position, and is equally intense on either side." No dark spots or vermiculations are present on the sides of head.

Pectoral fins clear and with no axillary blotch. Pelvic fins brown, the produced filaments of first soft rays very dark. Median fins pale dusky and variously spotted. Dark brown streaks lie on interradi al membrane anterior to each dorsal spine and are most prominent as continuations of the trunk bars, but no spots or mottling are present. The soft dorsal has a mottled appearance. The interradi al membranes are dusky and posteriorly overlain by pale spots. The anal is dusky with a few pale spots on last soft rays. Caudal fin is dusky with pale spots over entire fin.

Distribution

Although Günther (1862) recorded the type of *margaritiferum* from Lago Petén, Guatemala, Regan (1905; 1906-08) apparently distrusted these data and listed only "Guatemala" as type locality. P. H. Greenwood (personal communication) has kindly examined the British Museum of Natural History registers and indicates that "... the line which would be occupied by the type locality is left blank. The specimens listed before *C. margaritiferum*, registered on the same day and collected by Salvin, are given the locality of Isabella (and no other indication as to whether the place was a river or a lake name). The specimen immediately after *C. margaritiferum* is listed as coming from Lake Petén ..." Dr. Greenwood assumed that Günther either knew that *margaritiferum* came from Lago Petén or that he mis-read the register. The locality "Isabella" may refer to a

town on the Belize River several kilometers upriver from Belize. Godman (1915) related how Salvin, who collected the holotype, made three visits to Guatemala always by way of Belize, British Honduras. He spent some time near Belize and about three years collecting natural history specimens on both slopes of Guatemala. Thus, until additional specimens of *margaritiferum* are rediscovered, it is not even certain from which versant it came, although evidence suggests it is from the Atlantic slope of Guatemala or British Honduras.

Meristics.—Meristic summaries for each Population are presented in graphic form in figures 2 and 3. Counts for *C. margaritiferum* are indicated in the graphs, but not included in the following discussion of meristic variation. Although subject to considerable intraspecific variation, the mean spinous dorsal count for all three species is slightly greater than 16 (*robertsoni* 16.2, *longimanus* 16.1, *rostratum* 16.3). The mean dorsal soft-ray count is valuable in distinguishing *longimanus* (10.2) from *rostratum* (11.7); *robertsoni* (11.1) is intermediate.

C. robertsoni (6.1) averages about one less anal spine (6.1) than *longimanus* (7.0) or *rostratum* (6.9). In anal soft-rays, *robertsoni* averages a higher count (8.9 vs. *longimanus*, 8.0 and *rostratum*, 8.2).

C. rostratum (16.0) averages one more pectoral ray than *longimanus* (15.1) or *robertsoni* (15.0), and about two more gill rakers (19.3) than *longimanus* (17.5) and *robertsoni* (17.8).

Variation in number of pores of upper lateral line is great, although means for each species are very similar. *C. longimanus* (20.0) averages slightly less than *robertsoni* (20.5) and *rostratum* (20.5). *C. rostratum* (11.0) averages about one pore more in lower lateral line than *robertsoni* (10.2) or *longimanus* (10.0).

C. longimanus (27.7) averages slightly fewer longitudinal scales than *robertsoni* (28.2) or *rostratum* (28.2). *C. robertsoni* (6.1) averages about one more scale above lateral line than *rostratum* (5.0); *longimanus* (5.6) is intermediate. *C. rostratum* (16.2) averages almost two fewer scales around caudal peduncle than *robertsoni* (18.2) or *longimanus* (17.8).

Morphometrics.—Six proportional differences are sufficiently consistent to facilitate identification of the four species involved. These are orbit diameter, caudal fin length, interorbital distance, length of base of dorsal fin, least depth of caudal peduncle and predorsal distance. Data for the holotype of *margaritiferum* are included in each scatter graph (Figs. 4-7) and discussed below.

Their smaller orbit diameter and shorter caudal fin serves to distinguish *robertsoni* and *longimanus* (Populations C, D and E) from *rostratum* and Population F *longimanus* respectively (Figs. 4a, 4b, 5a and 5b). *C. margaritiferum*, the Finca Taboga specimens of *longimanus* and very large *robertsoni* are notable for their very small orbit diameter (Figs. 4a and 4b). *C. margaritiferum* resembles *robertsoni* and Populations C, D and E of *longimanus* with respect to caudal fin length.

C. rostratum has a shorter interorbital distance, length of base of dorsal fin and least depth of caudal peduncle than *longimanus* (Figs. 6a, 6b and 7a). Most *robertsoni* have a shorter interorbital distance than *longimanus*, but they exhibit more overlap due to greater variability than *rostratum*, hence individual plots are

excluded from Figure 6a. *C. margaritiferum* has a short interorbital distance and thus resembles *rostratum* and *robertsoni* in this respect.

C. robertsoni overlaps both *rostratum* and *longimanus* in length of dorsal fin base and is thus not considered in figure 6b. *C. margaritiferum* has a long dorsal fin base and most resembles *longimanus* in this character.

C. robertsoni lies intermediate to *rostratum* and *longimanus* in least depth of caudal peduncle. *C. margaritiferum* resembles *rostratum* in its narrow caudal peduncle (Fig. 7a).

C. rostratum has a greater predorsal distance than *robertsoni*. *C. longimanus* is quite variable in this respect and, therefore, is not included in figure 7b. *C. margaritiferum*, like *robertsoni*, has a shorter predorsal distance than *rostratum*.

DISCUSSION

Martin (1972), in his analysis of the Honduran ichthyofauna, considered *Cichlasoma popenoei* (= *C. longimanus*) part of a complement of species, extending along the xeric Pacific lowlands from Mexico to Nicaragua. He postulated that these species originated in western Mexico under dry climatic conditions during Miocene times, and that the spread of xeric climates southward along the west coast during the Pliocene and Pleistocene permitted its extension along Pacific Central America. *C. longimanus* could have gained access to the Atlantic slope as a result of stream capture between the Pacific Río Choluteca and Atlantic Río Patuca basins of Honduras. Headwater *longimanus* in each of these drainages are very similar and suggest a very recent connection in this area. Several other freshwater fishes occurring on both slopes in this region, probably utilized the same dispersal route.

Martin also suggested that *robertsoni* and six other *Cichlasoma* developed in the Petén-Yucatán region when the area may have been effectively isolated during much of the Upper Tertiary by the Chapayal Basin. Later, the species would have spread northward and southward along the Atlantic lowlands until attaining its present distribution.

We now believe that greater understanding of the histories of these species may be gained if we consider these four members of the *longimanus* complex to have evolved from a single widespread ancestral form. This is a reasonable assumption in view of the high degree of similarity between members of the complex. The distribution of this ancestral form is approximated by the present ranges of the three species (*margaritifer* is not included here because of its uncertain type locality) under consideration and perhaps by other forms not analyzed in this study. Subsequently, the precursor species of this monophyletic group was subdivided by natural barriers that persisted for a sufficient period to permit the evolution of descendent cognate forms. At present, no apparent physical barrier separates these cognate species but their ranges are contiguous, largely allopatric, and primarily confined to the Atlantic versant of Middle America. The Pacific slope populations of *longimanus* can be considered a secondary pattern of dis-

tribution, and since differentiation between Pacific and Atlantic populations is, at most, of a subspecific degree, this can be considered the result of a relatively recent dispersal through perhaps Honduran and Costa Rican routes.

A similar pattern of subdivision is found in several unrelated monophyletic lineages of Central American freshwater fishes. It appears that the Chapayal Basin and later the Amatique Embayment (Martin 1972) in southern Guatemala, and the Nicaraguan Depression (as a marine portal and perhaps later as an Atlantic marine embayment) isolated large segments of Middle America in Middle and Upper Tertiary times and will be discussed more fully in a forthcoming publication by Bussing. We postulate that *robertsoni* arose north of the Chapayal Basin, *rostratum* south of the Nicaraguan Depression, and that *longimanus* evolved between these two marine portals, all from a common ancestor. After the disappearance of these marine barriers, *robertsoni* has presumably replaced *longimanus* in northwestern Honduras and *rostratum* has retreated from its former range and into the Great Lakes Basin where it is now sympatric with *longimanus* (Fig. 8).

The allopatric Great Lakes Population of *longimanus* (F) was formerly connected with Population E in northern Costa Rica and/or with Population C in northern Nicaragua and Honduras (Fig. 1). The fact that several Atlantic Costa Rican fishes have invaded the Pacific versant of Costa Rica, presumably through a Río Sapoá-Río Tempisque dispersal route, would support a connection between Populations F and E. Morphologic and color traits provide no clue to the affinities of Great Lake *longimanus*, as this lacustrine population has developed an unique physiognomy in response to a lake environment, but a meristic comparison does provide a weak basis for favoring a former connection between Populations F and C. Of the 11 meristic traits considered (Figs. 2 and 3), eight reveal greater similarity between Populations F and C, two between F and E, and one shows no significant difference between the three Populations. On the basis of our proposed origin of the *longimanus* complex, we suspect that a former connection existed between Populations F and C and believe that future collections may produce specimens from this southern Nicaraguan hiatus. As already mentioned, gene exchange between Populations E and F across a northern Costa Rican dispersal route also is quite probable.

The single known specimen of *margaritiferum* appears to be closest to *longimanus*, but it also presents characters that are unique in the *Amphilophus* group. If *margaritiferum* were collected on the Pacific slope of Guatemala, it would fall into the present range of *longimanus*, although the specimens of *longimanus* we have examined from southern Guatemala show no tendency toward a *margaritiferum*-like morphotype. If the species were collected on the Atlantic slope, it would seem to represent a relict population presently cut off from *longimanus*. If additional material of this form is not forthcoming, it is conceivable that the species has become extinct since the holotype was collected over 110 years ago.

Additional evidence concerning its relationships points to an Atlantic slope locality for *margaritiferum*. The origins of the Middle American species groups of

Cichlasoma are unclear, but Regan (1905) has suggested certain South American species as related to some groups. No such related South American species are known for the *Amphilophus* or *Thorichthys* groups. Miller and Nelson recently (1961) defined the distinctive *Thorichthys* group, which is confined to the Atlantic slope of northern Middle America. Several *Amphilophus* group species share as many as five of the nine diagnostic *Thorichthys* traits and some have been erroneously assigned to the group (Meek 1907). *C. margaritifera*, while it does not conform to the diagnosis of Miller and Nelson (1961) and does not have the general appearance of a member of the *Thorichthys* group, it has two additional *Thorichthys* traits that are unique in the *Amphilophus* group: five sensory pores on the mandible and a subopercular blotch. Regan (1906-08) considered the *Thorichthys* group similar to *Amphilophus*. On the basis of the recognized similarity between the two species groups, and the discovery that *margaritifera* is apparently an intermediate form, we believe that *Amphilophus* gave rise to the *Thorichthys* group. Lago Petén would be a very reasonable locality in which to find a form intermediate to *Amphilophus* and *Thorichthys* group cichlids. Further speculation concerning derivation of these four species must await a comparative study of the genus *Cichlasoma*.

If one divides up most of the valid species of the *Amphilophus* group on a basis of general morphology, coloration, meristics and other traits, they fall into three complexes in Middle America and northern South America. The species distributions of each of these complexes are largely non-overlapping, and together, may trace the former widespread distribution of common ancestral forms. The complexes, based on an admittedly very superficial appraisal of the species, are as follows: 1) *C. longimanus* complex (*robertsoni*, *margaritifera*, *longimanus*, *rostratum*, *calobrense* and *altifrons*); 2) *C. labiatum* complex (*heterodontum*, *macracanthum*, *guija*, *labiatum*, *citrinellum* and *lyonsi*); 3) *C. ornatum* complex (*alfari*, *atromaculatum*, *ornatum* and *C. new species*). On the basis of its enlarged anterior teeth, rather large mouth and slim body profile, *C. ornatum* probably was placed in the *Parapetenia* group by Eigenmann (1910). This very real superficial resemblance between some of the small-mouthed members of the *Parapetenia* group and the *ornatum* complex of the *Amphilophus* group could be an important clue to the origin of the latter group.

Competition doubtless is important in determining the precise distribution of *longimanus*, *robertsoni* and *rostratum* today. That these species are nearly mutually exclusive suggests that competition between them is strong. *C. robertsoni* and *longimanus* are known from adjacent drainage basins in Honduras, but there is no evidence that they are sympatric at any point.

C. longimanus is widespread in Lago de Nicaragua, but *rostratum* is more restricted in distribution there. *C. rostratum*, however, replaces *longimanus* in the Río San Juan and other Costa Rican rivers. The lacustrine *longimanus* is apparently strongly adapted to standing water, and in rivers is found only in stagnant backwaters, whereas *rostratum* occurs in moving waters. Throughout the remainder of its range, and without *rostratum* to contend with, *longimanus* is generally found in waters of slow to moderate current velocity. Mayr (1963) in-

indicated that ecological differences are frequent between local populations of widespread species and particularly of peripherally isolated populations. To the north, *robertsoni* apparently occupies a niche similar to *longimanus*.

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SPECIMENS EXAMINED

Cichlasoma longimanus

Guatemala.—Esquintla: Río Colojate, 170 m, 34 specimens (USNM 114244, 114417, 203642); Suchitepequez: Río Nahualate drainage, 200 m, 2 specimens (UMMZ 188084).

El Salvador.—La Unión: Río Goascorán drainage, 100 m, 80 specimens (UCR 316-5). New record for El Salvador.

Honduras, Atlantic slope.—Yoro: Río Aguan drainage, 650 m, 1 specimen (LACM 32371-4); Olancho: Río Patuca drainage, 470 m, 189 specimens (LACM 32304-4, 32305-4, 32306-4, 32309-5, 32313-4, 32315-4, 32316-4, 32318-5, 32321-4, 32322-2); Gracias a Dios: Río Patuca drainage, 40 m, 94 specimens (LACM 32325-6, 32326-5, 32327-8, 32456-6, 32457-3, UCR 516-8); Río Coco drainage, 20 m, 36 specimens (LACM 32458-4, 32460-6); El Paraíso: Río Patuca drainage, 430 m, 4 specimens (LACM 32298-3, 32301-4).

Honduras, Pacific slope.—El Paraíso: Río Choluteca, 595 m, 12 specimens (UMMZ 144685); Francisco Morazán: Río Choluteca drainage, 735-790 m, 22 specimens (LACM

32302-5, 32324-4, UMMZ 144686, 188294); Choluteca: Choluteca drainage, 120-230 m, 12 specimens (LACM 32294-4, 322296-2, UCR 315-3); Valle: Río Nacaome, 30 m, 4 specimens (LACM 32295-4).

Nicaragua, Atlantic slope.—Zelaya: Río Wawa (Huahua) drainage, 10 m, 9 specimens (UCR 447-9, 448-7); Río Prinzapolka drainage, 350 m, 81 specimens (UCR 457-6); Madriz: Río Coco drainage, 700 m, 1 specimen (UCR 473-1); Estelí: Río Coco drainage, 850 m, 1 specimen (UCR 275-1); Boaco: Lago de Nicaragua drainage, 100 m, 1 specimen (UCR 265-4); León: Lago de Managua drainage, 40 m, 5 specimens (UCR 479-3); Managua: Laguna de Xiloá, 50 m, 15 specimens (UCR 276-1, 481-1); Masaya: Laguna de Masaya, 135 m, 20 specimens (UCR 189-3); Lago de Nicaragua: 31 m, 60 specimens (UCR 24-6, 468-1, 537-2, 538-1, 542-2, 546-2).

Nicaragua, Pacific slope.—León: Río Tamarindo, 40 m, 12 specimens (UCR 273-3, 464-4, 466-2, 477-1).

Costa Rica, Atlantic slope.—Guanacaste: Lago de Nicaragua drainage, 100 m, 1 specimen (UCR 125-6); Alajuela: Lago de Nicaragua drainage, 45 m, 65 specimens (UCR 245-5, 246-13).

Costa Rica, Pacific slope.—Guanacaste: Río Tempisque drainage, 20-70 m, 450 specimens (UCR 38-8, 133-8, 239-2, 455-1, 566-2); Río Bebedero drainage, 10-60 m, 253 specimens (UCR 9-2, 13-7, 134-7, 135-7, 151-4, 152-4, 153-1).

Cichlasoma rostratum

Nicaragua.—Lago de Nicaragua, 31 m, 48 specimens (UCR 24-5, 536-4, 542-1, 544-2, 546-1); Masaya: Laguna de Masaya, 135 m, 1 specimen (UCR 484-1).

Costa Rica.—Guanacaste: Río Sapoa drainage, 40-60 m, 63 specimens (UCR 122-17, 123-8, 124-10); Alajuela: Río Zapote drainage, 50 m, 56 specimens (UCR 248-5); Río San Carlos drainage, 70 m, 32 specimens (UCR 264-6); Heredia: Río Sarapiquí, 40 m, 18 specimens (LACM 9102-7, 9131-1, 9142-1, 9143-1, 9166-3, 9171-4, 9182-7, 9196-8); Limón: Río Madre de Dios drainage, 20 m, 4 specimens (UCR 444-5).

Cichlasoma robertsoni

México.—Veracruz: Río Coatzacoalcos drainage, 22-24 m, 55 specimens (UMMZ 187713, 187756, 187797).

British Honduras.—Belize: Belize River, 5-30 m, 21 specimens (UMMZ 159304); Mullins River, 4 specimens (MNHNP 9843, 9849); Toledo: Golden Stream, 40 m, 6 specimens (UCR 438-12, 440-14).

Guatemala.—El Petén: Lago Petén drainage, 115 m, 10 specimens (UMMZ 187424, MNHNP 5730); Río Sarstún, 25 m, 54 specimens (UMMZ 187978); Izabal: Río Sarstún drainage, 25 m, 31 specimens (USNM 114354); Río Polochic drainage, 5 specimens (MNHNP 9841, 9842); Río Motagua drainage, 25-85 m, 30 specimens (IU 11185, 11196, 11198, deposited at CAS).

Honduras.—Santa Bárbara: Río Ulua, 100-280 m, 103 specimens (LACM 32351-6, 32352-5, 32354-5, 32357-6, 32358-6, 32361-4); Cortés: Río Ulua drainage, 60-100 m, 140 specimens (LACM 32384-5, 32404-3, 32405-7, 32407-5, 32408-7, 32439-4, 32463-7, UCR 517-1); Atlantida: several short coastal streams, 10 m, 174 specimens (LACM 32374-5, 32435-5, 32453-5, 32454-4, 32461-7, 32462-3, UCR 515-11, 518-1); Yoro: Río Ulua drainage, 30-100 m, 143 specimens (LACM 32373-3, 32412-6, 32449-3, 32450-4, UCR 514-4).

RESUMEN

Cichlasoma longimanus, *C. margaritiferum*, *C. rostratum* y *C. robertsoni* forman un complejo dentro del grupo *Amphilophus*. Se revisa su historia taxonómica y se presenta las sinonimias correspondientes. Se reduce *Cichlasoma pop-*

enoei Carr y Giovannoli a la sinonimia de *C. longimanus*. *C. margaritifera*, sólo conocido del holotipo, se mantiene como una especie válida.

Se discute variación geográfica merística, morfométrica y de coloración, pero no se asigna nombres subespecíficos a las poblaciones. Para cada especie se describe la coloración en vida, dimorfismo sexual, características juveniles y su ecología. Se presenta una clave original para distinguir las cuatro especies.

Se analiza la importancia de eventos históricos y ecológicos-competencia para determinar la distribución geográfica actual.

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